GLOBAL DYNAMICS OF SOME POPULATION MODELS WITH SPATIAL DISPERSAL

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Global Dynamics of Some Population Models with Spatial Dispersal

by

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Abstract

Spatial evolution is a very important phenomenon in ecology and epidemiology. In mathematics, integro-difference/differential equations or reaction-diffusion equations are often used to describe different spatial spread/invasion phenomena. In this thesis, we investigate the global dynamics of some integro-difference and reaction-diffusion population models with spatial dispersal and temporal heterogeneities.

In Chapter 1, we present some basic terminologies and theorems which are used in this thesis. They are involved in monotone dynamics, spreading speeds and traveling waves, basic reproduction ratio, and chain transitive sets.

Chapter 2 is devoted to investigate the spatial dynamics for a class of discrete-time recursion systems, which describe the spatial propagation of two competitive invaders. The existence and global stability of bistable traveling waves are established for such systems under appropriate conditions.

In Chapter 3, we study spreading speeds and traveling waves for a class of reaction-diffusion equations with distributed delay. Such an equation describes growth and diffusion in a population where the individuals enter a quiescent phase exponentially and stay quiescent for some arbitrary time that is given by a probability density function. The existence of the spreading speed and its coincidence with the minimum wave speed of monostable traveling waves are established via the finite-delay approximation approach. We also prove the existence of bistable traveling waves in the

case where the associated reaction system admits a bistable structure. Moreover, the global stability and uniqueness of the bistable waves are obtained in the case where the density function has zero tail.

In Chapter 4, we investigate a periodic reaction-diffusion competition model, which describes the propagation of two competitive species in bad and good seasons. The existence and global stability of time-periodic bistable traveling waves are established for such a system under appropriate conditions.

In order to study the evolution dynamics of the Lyme disease in a periodic environment, in Chapter 5, we propose a reaction-diffusion Lyme disease model with seasonality. In the case of a bounded habitat, we obtain a threshold result on the global stability of either disease-free or endemic periodic solution. In the case of an unbounded habitat, we establish the existence of the disease spreading speed and its coincidence with the minimal wave speed for time-periodic traveling wave solutions. We also estimate parameter values based on some published data, and use them to study the Lyme disease transmission in Port Dove, Ontario.

In Chapter 6, we present a brief summary of this thesis and some future works.

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Chapter 1

Preliminaries

In this chapter, we present some terminologies and known results which will be used in this thesis. They are involved in monotone dynamical systems, spreading speed and traveling waves, basic reproduction ratios for periodic systems, and chain transitive sets.

1.1 Monotone dynamics

Let E be an ordered Banach space with an order cone P having nonempty interior $int(P)$. For any x, $y \in E$, we write $x \geq y$ if $x - y \in P$, $x > y$ if $x - y \in P \setminus \{0\}$ and $x \gg y$ if $x - y \in int(P)$. If $a < b$, we define the order interval $[a, b]_E := \{x \in E : a \leq x \leq b\}$.

Definition 1.1.1. *Let U be a subset of E, and $f : U \to U$ a continuous map. The map f is said to be monotone if $x \geq y$ implies that $f(x) \geq f(y)$; strictly monotone if $x > y$ implies that $f(x) > f(y)$; strongly monotone if $x > y$ implies that $f(x) \gg f(y)$.*

Theorem 1.1.1. (DANCER-HESS CONNECTING ORBIT THEOREM) [9, PROPOSITION 1] *Let $u_1 < u_2$ be fixed points of the strictly monotone continuous mapping $f : U \to U$,* *let* $I := [u_1, u_2] \subset U$, *and assume that* $f(I)$ *is precompact and that* f *has no fixed point distinct from* u_1 *and* u_2 *in* I. *Then either*

(a) *there exists an entire orbit* $\{x_n\}_{n=-\infty}^{\infty}$ *of* f *in* I *such that* $x_{n+1} > x_n$, $\forall n \in \mathbb{N}$, *and* $\lim_{n\to-\infty} x_n = u_1$ *and* $\lim_{n\to\infty} x_n = u_2$, *or*

(b) *there exists an entire orbit* $\{y_n\}_{n=-\infty}^{\infty}$ *of* f *in* I *such that* $y_{n+1} < y_n$, $\forall n \in \mathbb{N}$, *and* $\lim_{n\to-\infty} y_n = u_2$ *and* $\lim_{n\to\infty} = u_1$.

Recall that a subset K of E is said to be order convex if $[u, v] \in K$ whenever $u, v \in K$ satisfy $u < v$.

Definition 1.1.2. *Let* $U \subset P$ *be a nonempty, closed and order convex set. A continuous map* $f : U \to U$ *is said to be subhomogeneous if* $f(\lambda x) \geq \lambda f(x)$ *for any* $x \in U$ *and* $\lambda \in [0, 1]$; *strictly subhomogeneous if* $f(\lambda x) > \lambda f(x)$ *for any* $x \in U$ *with* $x \gg 0$ *and* $\lambda \in (0, 1)$; *strongly subhomogeneous if* $f(\lambda x) \gg \lambda f(x)$ *for any* $x \in U$ *with* $x \gg 0$ *and* $\lambda \in (0, 1)$.

Let M be a metric space with metric d and $f : M \to M$ a continuous map. f is said to be asymptotically smooth if for any nonempty closed bounded set $B \subset M$ for which $f(B) \subset B$, there is a compact set $J \subset B$ such that J attracts B, that is, $\limsup_{n\to\infty} \sup_{x\in B} \{d(f^n(x), J)\} = 0$. The omega limit set of $x \in M$ is defined by $\omega(x) = \{y \in M : f^{n_k}(x) \to y$, for some $n_k \to \infty\}$. Denote the Fréchet derivative of f at $u = a$ by $Df(a)$ if it exists, and let $r(Df(a))$ be the spectral radius of the linear operator $Df(a) : E \to E$.

Theorem 1.1.2. [67, THEOREM 2.2.4] *Let* U *be a closed and order convex subset of an ordered Banach space* E *with nonempty positive cone, and* $f : U \to U$ *continuous and monotone. Assume that there exists a monotone homeomorphism* h *from* $[0, 1]$ *onto a subset of* U *such that*

(1) For each $s \in [0,1], h(s)$ *is a stable fixed point for* $f : U \to U$*;*

(2) Each forward orbit of f *on* $[h(0), h(1)]_E$ *is precompact;*

(3) One of the following two properties holds:

(3a) If $\omega(\phi) > h(s_0)$ *for some* $s_0 \in [0,1)$ *and* $\phi \in [h(0), h(1)]_E$*, then there exists* $s_1 \in (s_0, 1)$ *such that* $\omega(\phi) \geq h(s_1)$*;*

(3b) If $\omega(\phi) < h(r_1)$ *for some* $r_1 \in (0,1]$ *and* $\phi \in [h(0), h(1)]_E$*, then there exists* $r_0 \in (0, r_1)$ *such that* $\omega(\phi) \leq h(r_0)$*.*

Then for any precompact orbit $\gamma^+(y)$ *of* f *in* U *with* $\omega(y) \bigcap [h(0), h(1)]_E \neq \emptyset$*, there exists* $s^* \in [0,1]$ *such that* $\omega(y) = h(s^*)$*.*

Theorem 1.1.3. (Threshold dynamics) [67, Theorem 2.3.4] *Let either* $V = [0, b]_E$ *with* $b \gg 0$ *or* $V = P$*. Assume that*

(1) $f : V \to V$ *satisfies either*

(i) f *is monotone and strongly subhomogeneous; or*

(ii) f *is strongly monotone and strictly subhomogeneous;*

(2) $f : V \to V$ *is asymptotically smooth, and every positive orbit of* f *in* V *is bounded;*

(3) $f(0) = 0$*, and* $Df(0)$ *is compact and strongly positive.*

Then there exists threshold dynamics:

(a) If $r(Df(0)) \leq 1$*, then every positive orbit in* V *converges to 0;*

(b) If $r(Df(0)) > 1$*, then there exists a unique fixed point* $u^* \gg 0$ *in* V *such that every positive orbit in* $V \setminus \{0\}$ *converges to* u^**.*

Next we briefly review monotone delay differential equations. Let r denote the maximal delay appearing in the equation, and space C be a set of all continuous functions from $[-r, 0]$ to $\mathbb{R}^n$ with cone $C_+ = \{\phi \in C : \phi(\theta) \geq 0, -r \leq \theta \leq 0\}$. The notation $\leq, <, \ll$ denote the order relations on C generated by C_+. Let D be an open subset of C and $f : D \to \mathbb{R}^n$ is continuous. Then we say f is quasimonotone if f satisfies the following condition:

(Q) $f_i(\phi) \leq f_i(\psi)$ whenever $\phi \leq \psi$ and $\phi_i(0) = \psi_i(0)$ holds for some i.

For a general nonautononous linear delay differential equation

$$x'(t) = L(t)x_t \tag{1.1}$$

where $L : \mathbb{R} \to L(C, \mathbb{R}^n)$ is continuous and $L(C, \mathbb{R}^n)$ is the space of bounded linear maps from C into $\mathbb{R}^n$. Then $L(t)$ satisfies (Q) condition if and only if the following condition holds:

(K) $L_i(t)\phi \geq 0$ whenever $\phi \geq 0$ and $\phi_i(0) = 0$, where $L_i(t)\phi$ denotes the ith component of $L(t)\phi$.

Lemma 1.1.1. [52, Lemma 5.1.2] *Condition (K) holds if and only if there exists $a_i(t)$ for $1 \leq i \leq n$ and positive Borel measures $\eta_{ij}(t)$ for $1 \leq i, j \leq n$ such that*

$$L_i(t)\phi = a_i(t)\phi_i(0) + \sum_{j=1}^{n} \int_{-r}^{0} \phi_j(\theta) d_\theta \eta_{ij}(t, \theta), \tag{1.2}$$

and $\eta_{ij}(t)\{0\} = 0$. Moreover, if (K) holds then the representation (1.2) *is unique and $a_i(t)$ and $\eta_{ij}(t)$ are continuous functions of t.*

Lemma 1.1.2. [52, Lemma 5.3.2] *Let (K) and the following two conditions hold:*

(R) For each j for which $r_j > 0$, there exists i such that for all $t, \eta_{ij}(t)([-r_i, -r_j + \epsilon]) > 0$ for all small $\epsilon > 0$.

(I) The matrix $A(L)(t)$ defined by $A(L)(t) = col(L(t)\hat{e}_1, ..., L(t)\hat{e}_n)$ is irreducible. If $\phi > 0$ and t_0 are given, then the solution of (1.1) $x(t, t_0, \phi) \gg 0$ *for* $t \geq t_0 + nr$.

Let D be an open subset of C_r, and $f : D \to \mathbb{R}^n$ be continuously differentiable. We say delay differential equation

$$x'(t) = f(x_t) \tag{1.3}$$

is cooperative if D is order convex and $df(\phi)$ satisfies (K) for each $\phi \in D$. System (1.3) is cooperative and irreducible if it is cooperative and the following hold:

(1) $df(\phi)$ satisfies (I) for each $\phi \in D$.

(2) For every j for which $r_j > 0$, there exists i such that for all $\phi \in D$, $\eta_{ij}(\phi)([-r_j, -r_j + \epsilon)) > 0$ for all small $\epsilon > 0$.

Theorem 1.1.4. [52, THEOREM 5.3.4] *If* (1.3) *is cooperative and irreducible in D, and $\phi, \psi \in D$ satisfy $\phi < \psi$, then $x(t, \phi) \ll x(t, \psi)$ for all $t \geq nr$.*

In order to address the stability of the equilibria of (1.3), we assume function f is continuously differentiable and cooperative in D. Suppose $\hat{v}$ is an equilibrium of (1.3), that is, $v \in \mathbb{R}^n$, is such that $\hat{v} := (v, ..., v) \in D$ and $f(\hat{v}) = 0$. Then the variational system corresponding to $\hat{v}$ is

$$y'(t) = Ly_t, \;\; L = df(\hat{v}). \tag{1.4}$$

Let $y(t) = e^{\lambda t}u$ be a solution of (1.4), where $u \in \mathbb{R}^n$, then λ must be a root of $Det\Delta(\lambda) = 0$, where $\Delta(\lambda) = \lambda I - A(\lambda)$ and $A(\lambda)_{ij} = a_i\delta_{ij} + \int_{-r_j}^{0} e^{\lambda\theta} d\eta_{ij}(\theta)$. Define the stability modulus of L as

$$s(L) = \max\{Re\lambda : Det\Delta(\lambda) = 0\}.$$

Then we say $\hat{v}$ is asymptotically stable if $s(L) < 0$ and unstable if $s(L) > 0$.

If we ignore any delays in (1.3), we get the following cooperative and irreducible system of ordinary differential equations:

$$x' = F(x), \quad F(x) = f(\hat{x}). \tag{1.5}$$

Observe that (1.5) has the same equilibria as (1.3). Then the following result shows that v is asymptotically stable (unstable) for the ODE system (1.5) if and only if $\hat{v}$ is asymptotically stable (unstable) for the FDE system (1.3).

Lemma 1.1.3. [52, COROLLARY 5.5.2] $s(L) < 0$ $(s(L) > 0)$ *if and only if* $s(DF(\hat{v})) < 0$ $(s(DF(\hat{v}) > 0)$.

1.2 Spreading speeds and traveling waves

1.2.1 Spreading speed and monostable waves

Let $\mathbb{C}$ be the set of all bounded and continuous functions from $\mathbb{H}$ to $\mathbb{R}^k$ with the cone $\mathbb{R}^k_+$, where $\mathbb{H} = \mathbb{R}$ or $\mathbb{Z}$. Clearly, every vector in $\mathbb{R}^k$ can be regarded as a function in $\mathbb{C}$. For $u = (u_1, ...u_k)$, $w = (w_1, ...w_k) \in \mathbb{C}$, we write $u \geq w(u \gg w)$ provided that $u_i(x) \geq w_i(x)(u_i(x) > w_i(x), \forall i = 1, ...k, \forall x \in \mathbb{H}$, and $u > w$ provided $u \geq w$ but $u \neq w$. For any $r \gg 0$, we define

$$\mathbb{R}^k_r := \{u \in \mathbb{R}^k : 0 \leq u \leq r\} \text{ and } \mathbb{C}_r := \{u \in \mathbb{C} : 0 \leq u \leq r\}.$$

We equip $\mathbb{C}$ with the compact open topology, which can be given in the following sense: $u^m \to u$ in $\mathbb{C}$ means that the sequence $u^m(x)$ converges to $u(x)$ uniformly for x in any compact set in $\mathbb{H}$. We equip $\mathbb{C}$ with the norm with respect to this topology by the following distance function:

$$d(u,w) := \sum_{k=1}^{\infty} \frac{\max_{|x|\leq k} |u(x) - w(x)|}{2^k}, \ \forall u, w \in \mathbb{C},$$

where $|\cdot|$ denotes the usual norm in the space $\mathbb{R}^k$, then $(\mathbb{C}, d)$ is a metric space.

Define the reflection operator $\mathcal{R}$ by $\mathcal{R}[u](x) = u(-x)$. Given any $y \in \mathbb{H}$, define the translation operator T_y by $T_y[u](x) := u(x-y)$. Let $\beta \gg 0$ in $\mathbb{R}^k$ and $Q : \mathbb{C}_\beta \to \mathbb{C}_\beta$ be given. In order to present the theory developed in [28, 27, 29], we introduce the following assumptions:

(A1) $Q[\mathcal{R}[u]] = \mathcal{R}[Q[u]]$, $T_y \circ Q[u] = Q \circ T_y[u]$, $\forall u \in \mathbb{C}_\beta$, $y \in \mathbb{H}$.

(A2) $Q : \mathbb{C}_\beta \to \mathbb{C}_\beta$ is continuous with respect to the compact open topology.

(A3) Q is order preserving in the sense that $Q[u] \geq Q[v]$ whenever $u \geq v$ in $\mathbb{C}_\beta$.

(A4) $Q : \mathbb{R}^k_\beta \to \mathbb{R}^k_\beta$ admits exactly two fixed points 0 and β, and $\lim_{n\to\infty} Q^n[\alpha] = \beta$ for any $\alpha \in \mathbb{R}^k_\beta$ with $0 \ll \alpha \leq \beta$.

Given a function $\phi \in \mathbb{C}_\beta$ and a bounded interval $I = [a,b] \subset \mathbb{R}$, we define a function $\phi_I \in C(I, \mathbb{R}^k)$ by $\phi_I(x) = \phi(x)$. Moreover, for any subset $\mathbb{D}$ of $\mathbb{C}_\beta$, we define $\mathbb{D}_I = \{\phi_I \in C(I, \mathbb{R}^k) : \phi \in \mathbb{D}\}$. We need the following weak compactness assumption:

(A5) For any $\delta > 0$, there exists $l = l(\delta) \in [0,1)$ such that for any $\mathbb{D} \subset \mathbb{C}_\beta$ and any interval $I = [a,b]$ of the length δ, we have $\alpha(Q[\mathbb{D}]_I) \leq l\alpha(\mathbb{D}_I)$, where α is the Kuratowski measure of noncompactness on the Banach space $C(I, \mathbb{R}^k)$.

Note that the standing assumptions (A4) and (A5) are weaker than those (A5) and (A6) in [28] and [27], respectively. According to [29], all the results in [28, 27] are still valid under the above assumptions (A1)-(A5).

Theorem 1.2.1. [28, THEOREM 2.11, THEOREM 2.15 AND CORALLARY 2.16] *Suppose that Q satisfies (A1)-(A5). Let $u_0 \in \mathbb{C}_\beta$ and $u_n = Q[u_{n-1}]$ for $n \geq 1$. Then there is a real number c^* such that the following statements are valid:*

(i) For any $c > c^*$, if $0 \leq u_0 \ll \beta$ and $u_0(x) = 0$ for x outside a bounded interval, then $\lim_{n\to\infty, |x|\geq nc} u_n(x) = 0$.

(ii) For any $c < c^*$ and any $\sigma \in [0, r]$ with $\sigma \gg 0$, there exits $r_\sigma > 0$ such that if $u_0(x) \geq \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{n\to\infty, |x|\leq nc} u_n(x) = \beta$. If, in addition, Q is subhomogeneous on $\mathbb{C}_\beta$, then r_σ can be chosen to be independent of $\sigma \gg 0$

We call c^* in the above theorem the asymptotic speed of spread (in short, spreading speed) of the map Q on $\mathbb{C}_\beta$. In order to estimate the spreading speed c^*, a linear operator approach was developed in [28]. Let $M : \mathbb{C} \to \mathbb{C}$ be a linear operator with the following properties:

(B1) M is continuous with respect to the compact open topology.

(B2) M is a positive operator, that is, $M[u] \geq 0$ whenever $u > 0$.

(B3) M satisfies (A5) with $\mathbb{C}_\beta$ replaced by any subset of $\mathbb{C}$ consisting of uniformly bounded functions.

(B4) $M[\mathcal{R}[u]] = \mathcal{R}[M[u]]$, $T_y[M[u]] = M[T_y[u]], \forall u \in \mathbb{C}, y \in \mathbb{H}$.

(B5) M can be extended to a linear operator on the linear space $\tilde{C}$ of all functions $u \in C(\mathbb{H}, \mathbb{R}^k)$ having the form

$$u(x) = v_1(x)e^{\mu_1 x} + v_2(x)e^{\mu_2 x}, v_1, v_2 \in \mathbb{C}, \mu_1, \mu_2 \in \mathbb{R}, x \in \mathbb{H}$$

such that if $u_n, u \in \mathbb{C}$ and $u_n(x) \to u(x)$ uniformly on any bounded set, then $M[u_n](x) \to M[u](x)$ uniformly on any bounded set.

Note that hypothesis (B4) implies that M is also a linear operator on $\mathbb{R}^k$. Define the linear map $B_\mu : \mathbb{R}^k \to \mathbb{R}^k$ by

$$B_\mu[\sigma] = M[\sigma e^{-\mu x}](0), \forall \sigma \in \mathbb{R}^k.$$

In particular, $B_0 = M$ on $\mathbb{R}^k$. If $\sigma_n, \sigma \in \mathbb{R}^k$ and $\sigma_n \to \sigma$ as $n \to \infty$, then $\sigma_n e^{-\mu x} \to \sigma e^{-\mu x}$ uniformly on any bounded subset of $\mathbb{H}$. Thus, $B_\mu[\sigma_n] = M[\sigma_n e^{-\mu x}](0) \to M[\sigma e^{-\mu x}](0) = B_\mu[\sigma]$, and hence B_μ is continuous. Moreover, B_μ is a positive operator on $\mathbb{R}^k$. Assume that

(B6) For any $\mu > 0, B_\mu$ is positive, and there is an n_0 such that $B_\mu^{n_0} = \underbrace{B_\mu B_\mu ... B_\mu}_{n_0}$ is a compact and strongly positive linear operator on $\mathbb{R}^k$.

It then follows from [28, Lemma 3.1] that B_μ has a principal eigenvalue $\lambda(\mu)$ with a strongly positive eigenfunction. The following condition is needed for the estimate of the spreading speed c^*.

(B7) The principal eigenvalue $\lambda(0)$ of B_0 is larger than 1.

Define $\Psi(\mu) := \frac{\ln \lambda(\mu)}{\mu}, \forall \mu > 0$. From [28, Lemma 3.8], we know that $\Psi(\mu)$ admits the following properties:

Lemma 1.2.1. [28, Lemma 3.8] *The following statements are valid:*

(i) $\Psi(\mu) \to \infty$ *as* $\mu \to 0^+$.

(ii) $\Psi(\mu)$ *is decreasing near 0.*

(iii) $\Psi'(\mu)$ *changes sign at most once on* $(0, \infty)$.

Then we can use the following result to estimate the spreading speed of Q.

Theorem 1.2.2. [28, THEOREM 3.10] *Let Q be an operator on $\mathbb{C}_\beta$ satisfying (A1)-(A5) and c^* be the asymptotic speed of spread of Q. Assume that the linear operator M satisfies (B1)-(B7), and either M has compact support or the infimum of $\Psi(\mu)$ is attained at some finite value μ^* and $\Psi(+\infty) > \Psi(\mu^*)$. Then the following statements are valid:*

(1) *If $Q[u] \leq M[u]$ for all $u \in \mathbb{C}_\beta$, then $c^* \leq \inf_{\mu>0} \Psi(\mu)$.*

(2) *If there is some $\eta \in \mathbb{R}^k$, with $\eta \gg 0$, such that $Q[u] \geq M[u]$ for any $u \in \mathbb{C}_\eta$, then $c^* \geq \inf_{\mu>0} \Psi(\mu)$*

For the existence and nonexistence traveling waves, we have the following result:

Theorem 1.2.3. [28, THEOREMS 4.1 AND 4.2] *Let Q satisfies (A1)-(A5), and let c^* be the spreading speed of Q. Then*

(1) *For any $c < c^*$, Q has no traveling wave $W(x - cn)$ connecting β to 0.*

(2) *For any $c \geq c^*$, Q has a traveling wave $W(x - cn)$ connecting β to 0 such that $W(x)$ is nondecreasing in x.*

Recall that a family of mappings $\{Q_t\}_{t\geq 0}$ is said to be an T-periodic semiflow on space $\mathbb{C}$ provided that it has the following properties:

(i) $Q_0[\phi] = \phi$, $\forall \phi \in \mathbb{C}$.

(ii) $Q_t \circ Q_T[\phi] = Q_{t+T}[\phi]$, $\forall \phi \in \mathbb{C}$.

(iii) $Q_t[\phi]$ is continuous jointly in (t, ϕ) on $[0, \infty) \times \mathbb{C}$.

The mapping Q_T is called the Poincaré map associated with this periodic semiflow.

Based on the theory of spreading speeds and traveling waves for periodic semiflows in the monostable case [27], we have the following result on the existence of spreading speeds for periodic semiflows.

Theorem 1.2.4. [27, THEOREM 2.1] *Let $\{Q_t\}_{t\geq 0}$ be a T-periodic semiflow on $\mathbb{C}_r$ with two x-independent T-periodic orbits $0 \ll u^*(t)$. Suppose that the Poincare map $Q = Q_T$ satisfies all hypotheses (A1)-(A5) with $\beta = u^*(0)$, and Q_t satisfies (A1) for any $t > 0$. Let c^* be the asymptotic speed of spread for Q_T. Then the following statements are valid:*

(1) For any $c > \frac{c^*}{T}$, if $v \in \mathbb{C}_\beta$ with $0 \leq v \ll \beta$, and $v(x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\geq tc} Q_t[v](x) = 0$.

(2) For any $c < \frac{c^*}{T}$ and any $\sigma \in [0, r]$ with $\sigma \gg 0$, there exists a positive number $r_\sigma > 0$ such that if $v \in \mathbb{C}_\beta$ and $v(x) \gg \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{t\to\infty, |x|\leq tc}(Q_t[v](x) - u^*(t)) = 0$. If, in addition, Q_T is subhomogeneous on $\mathbb{C}_\beta$, then r_σ can be chosen to be independent of $\sigma \gg 0$.

We say that $W(t, x - ct)$ is a periodic traveling wave of the T-periodic semiflow $\{Q_t\}_{t\geq 0}$ if the vector-valued function $W(t, z)$ is T-periodic in t and $Q_t[W(0,\cdot)](x) = W(t, x - ct)$, and that $W(t, x - ct)$ connects $u^*(t)$ to 0 if $W(t, -\infty) = u^*(t)$ and $W(t, +\infty) = 0$ uniformly for $t \in [0, T]$. As usual, we call c the wave speed, and $W(t, z)$ the wave profile.

Theorem 1.2.5. [27, THEOREMS 2.2 AND 2.3] *Let $\{Q_t\}_{t\geq 0}$ be a T-periodic semiflow on $\mathbb{C}_r$ with two x-independent T-periodic orbits $0 \ll u^*(t)$. Suppose that the Poincaré map $Q = Q_T$ satisfies all hypotheses (A1)-(A5) with $\beta = u^*(0)$. Let c^* be the asymptotic speed of spread for Q_T. Then the following statements are valid:*

(1) For any $0 < c < \frac{c^*}{T}$, $\{Q_t\}_{t\geq 0}$ has no T-periodic traveling wave $W(t, x - ct)$ connecting $u^*(t)$ to 0.

(2) If, in addition, Q_t satisfies (A1) and (A3) for each $t > 0$, then for any $c \geq \frac{c^*}{T}$, $\{Q_t\}_{t\geq 0}$ has an T-periodic traveling wave $W(t, x-ct)$ connecting $u^*(t)$ to 0 such that $W(t, z)$ is continuous, and nonincreasing in $z \in \mathbb{R}$.

1.2.2 Bistable waves

Let $\mathcal{X}$ be an ordered Banach space with the norm $\|\cdot\|_{\mathcal{X}}$ and cone $\mathcal{X}^+$ with nonempty interior, and $\mathcal{C}$ be the set of all bounded and continuous function from $\mathcal{H}$ to $\mathcal{X}$ equipped with the compact open topology, where $\mathcal{H} = \mathbb{R}$ or $\mathbb{Z}$.

Let $\beta \in int\mathcal{X}^+$ and Q be a map from $\mathcal{C}_\beta$ to $\mathcal{C}_\beta$ with $Q(0) = 0$ and $Q(\beta) = \beta$. Let E be the set of all fixed points of Q restricted on $\mathcal{X}_\beta$. Assume that Q satisfies the following assumptions:

(C1) (*Translation invariance*) $T_y \circ Q[\phi] = Q \circ T_y[\phi]$, $\forall \phi \in \mathcal{C}_\beta$, $y \in \mathbb{H}$, where T_y is defined by $T_y[\phi](x) = \phi(x - y)$.

(C2) (*Continuity*) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is continuous with respect to the compact open topology.

(C3) (*Monotonicity*) Q is order preserving in the sense that $Q[\phi] \geq Q[\psi]$ whenever $\phi \geq \psi$ in $\mathcal{C}_\beta$.

(C4) (*Compactness*) $Q : \mathcal{C}_\beta \to \mathcal{C}_\beta$ is compact with respect to the compact open topology.

(C5) (*Bistability*) Two fixed points 0 and β are strongly stable from above and below, respectively, for the map $Q : \mathcal{X}_\beta \to \mathcal{X}_\beta$, that is, there exist a number $\delta > 0$ and unit vectors e_1 and $e_2 \in int(\mathcal{X}^+)$ such that

$$Q[\eta e_1] \ll \eta e_1, \; Q[\beta - \eta e_2] \gg \beta - \eta e_2, \; \forall \eta \in (0, \delta],$$

and the set $E \setminus \{0, \beta\}$ is totally unordered.

(C6) (*Counter-propagation*) For each $\alpha \in E \setminus \{0, \beta\}$, $c_-^*(\alpha, \beta) + c_+^*(0, \alpha) > 0$, where $c_-^*(\alpha, \beta)$ and $c_+^*(0, \alpha)$ represent the leftward and rightward spreading speeds of monostable subsystem $\{Q^n\}_{n \geq 0}$ restricted on $[\alpha, \beta]_{\mathcal{C}}$ and $[0, \alpha]_{\mathcal{C}}$, respectively.

Theorem 1.2.6. [13, THEOREM 3.1] *Assume that Q satisfies (C1)-(C6). Then there exists $c \in \mathbb{R}$ such that the discrete semiflow $\{Q^n\}_{n \geq 1}$ admits a nondecreasing traveling wave with speed c and connecting 0 to β, that is, there exists a nondecreasing function $\varphi \in \mathcal{C}$ such that $Q^n[\varphi](x) = \varphi(x - cn), \forall x \in \mathcal{H}, n \geq 0$ with $\varphi(-\infty) := \lim_{x \to -\infty} \varphi(x) = 0$ and $\varphi(+\infty) := \lim_{x \to +\infty} \varphi(x) = \beta$.*

Let $\omega \in \mathcal{T}$ be a positive number, where $\mathcal{T} = \mathbb{R}^+$ or $\mathbb{Z}^+$, and $\{Q_t\}_{t \in \mathcal{T}}$ be an ω-time periodic semiflow on a metric subspace of $\mathcal{C}$ with the Poincaré map Q_ω. Then for time-periodic semiflow, we have the following result.

Theorem 1.2.7. [13, THEOREM 3.3] *Let $\beta(t)$ be a strongly positive ω-time periodic orbit of $\{Q_t\}_{t \in \mathcal{T}}$ restricted on $\mathcal{X}$. Assume that $Q := Q_\omega$ satisfies the assumptions (C1)-(C6) with $\beta = \beta(0)$. Then $\{Q_t\}_{t \in \mathcal{T}}$ admits a traveling wave $U(t, x + ct)$ with $U(t, -\infty) = 0$ and $U(t, \infty) = \beta(t)$ uniformly for $t \in \mathcal{T}$. Furthermore, $U(t, x)$ is nondecreasing in $x \in \mathbb{R}$.*

Let $\tau > 0$ be a fixed real number. Choose $\mathcal{X} := C([-\tau, 0], \mathbb{R})$, $\mathcal{Y} := C(\mathbb{R}, \mathbb{R})$ and $\mathcal{C} := C([-\tau, 0], \mathcal{Y})$. Consider the existence of the bistable traveling waves of the following and time-delayed reaction-diffusion equation:

$$\begin{cases} \dfrac{\partial u(t,x)}{\partial t} = d \dfrac{\partial^2 u(t,x)}{\partial x^2} + f(u_t)(x), & t > 0, \ x \in \mathbb{R} \\ u_0 = \phi \in \mathcal{C}, & \theta \in [-\tau, 0], \end{cases} \tag{1.6}$$

where $f : \mathcal{C} \to \mathcal{Y}$ is Lipschitz continuous and for each $t \geq 0$, $u_t \in \mathcal{C}$ is defined by $u_t(\theta, x) := u(t + \theta, x)$, $\forall \theta \in [-\tau, 0]$, $x \in \mathbb{R}$.

Define $\bar{f} : \mathcal{X} \to \mathbb{R}$ by $\bar{f}(\phi) = f(\phi)$ and $\hat{f} : \mathbb{R} \to \mathbb{R}$ by $\hat{f}(\xi) = f(\xi)$. In order to obtain the existence of the bistable waves for system (1.6), we impose the following assumptions on f:

(D1) $0 < \alpha < \beta$ are three equilibria and there are no other equilibria between 0 and β.

(D2) The functional $f : \mathcal{C}_\beta \to \mathcal{Y}$ is quasi-monotone in the sense that whenever $\phi \geq \psi$ in $\mathcal{C}_\beta$,

$$\lim_{h\to 0^+} \frac{1}{h} d([\phi(0) - \psi(0)] + h[f(\phi) - f(\psi)]; \mathcal{Y}_+) = 0.$$

(D3) Equilibria 0 and β are stable, and α is unstable in the sense that $\hat{f}'(0) < 0$, $\hat{f}'(\alpha) > 0$ and $\hat{f}'(\beta) < 0$.

(D4) For each $\phi \in \mathcal{X}_\beta$, the derivative $\bar{L}(\phi) := D\bar{f}(\phi)$ of $\bar{f}$ can be represented as

$$\bar{L}(\phi)\psi = a(\phi)\psi(0) + \int_{-\tau}^{0} \psi(\theta) d_\theta \eta(\phi) := a(\phi)\psi(0) + L_1(\phi)\psi,$$

where $\eta(\phi)$ is a positive Borel measure on $[-\tau, 0]$ and $\eta(\phi)([-\tau, -\tau + \epsilon]) > 0$ for all small $\epsilon > 0$.

(D5) For any small $\epsilon > 0$, there exists a number $\delta \in (0, \beta)$ and a linear operator $L_\epsilon : \mathcal{C}_\beta \to \mathcal{Y}$ such that $L_\epsilon \phi \to Df(\alpha)\phi$, $\forall \phi \in \mathcal{C}_\beta$, as $\epsilon \to 0$ and that

$$f(\alpha + \phi) \geq L_\epsilon(\phi), \text{ and } f(\alpha - \phi) \leq -L_\epsilon(\phi), \ \forall \phi \in \mathcal{C}_\delta.$$

Theorem 1.2.8. [13, THEOREM 6.4] *Under assumptions (D1)-(D5), system* (1.6) *admits a nondecreasing traveling wave* $\varphi(x + ct)$ *with* $\varphi(-\infty) = 0$ *and* $\varphi(+\infty) = \beta$.

Remark 1.2.1. *Theorems 1.2.6-1.2.8 are still valid provided that the ordered fixed points $0 \ll \beta$ are replaced by two ordered fixed points $\beta_1 \ll \beta_2$ in $\mathcal{X}$, and $\mathcal{X}_\beta$ and $\mathcal{C}_\beta$ are replaced by $[\beta_1, \beta_2]_\mathcal{X}$ and $[\beta_1, \beta_2]_\mathcal{C}$, respectively.*

1.3 Basic reproduction ratios for periodic systems

The basic reproduction ratio R_0 is a very important concept in study the spread of communicable disease, which is defined as the expected number of secondary cases produced in a completely susceptible population by a typical infective individual. In many cases, it is expected to be a threshold parameter, that is, one may expect the disease can invade the susceptible population if $R_0 > 1$, and the disease may die out if $R_0 < 1$.

In this section, we present the theory of basic reproduction ratios for compartmental epidemic models in periodic environments which was developed in [3, 59]. We consider a heterogeneous population whose individual can be divided into two types: infected compartments, labeled by $i = 1, 2, \ldots, m$, and uninfected compartments, labeled by $i = m+1, \ldots, n$. Define X_s to be the set of all disease-free states

$$X_s := \{x \geq 0 : x_i = 0, \forall i = 1, 2, \ldots, m\}.$$

Let $\mathcal{F}_i(t, x)$ be the input rate of newly infected individuals in the $i-$th compartment, $\mathcal{V}_i^+(t, x)$ be the input rate of individuals by other means(for example, births, immigrations), and $\mathcal{V}_i^-(t, x)$ be the rate of transfer of individuals out of compartment i (for example, deaths, recovery and emigrations). Thus, the disease transmission model in a periodic environment is governed by a periodic ordinary differential system:

$$\frac{dx_i}{dt} = \mathcal{F}_i(t, x) - \mathcal{V}_i(t, x) := f_i(t, x), i = 1, \ldots, n, \tag{1.7}$$

where $\mathcal{V}(t,x) = \mathcal{V}_i^-(t,x) - \mathcal{V}_i^+(t,x)$. Assume that the model (1.7) has an infection-free periodic solution $x^0(t) = x(0,\ldots,0,x_{m+1}^0(t),\ldots,x_n^0(t))^T$ with $x_i^0(t) > 0, m+1 \leq i \leq n$ for all t. Let $f = (f_1,\ldots,f_n)^T$, and define the following matrices

$$M(t) := (\frac{\partial f_i(t,x^0(t))}{\partial x_j})_{m+1 \leq i,j \leq n}, \quad F(t) := (\frac{\partial \mathcal{F}_i(t,x^0(t))}{\partial x_j})_{1 \leq i,j \leq m},$$

and

$$V(t) := (\frac{\partial \mathcal{V}_i(t,x^0(t))}{\partial x_j})_{1 \leq i,j \leq m}.$$

Denote $\Phi_P(t)$ be the monodromy matrix for the periodic system $\frac{dz}{dt} = P(t)z$. Assume that

(E1) For each $1 \leq i \leq n$, the function $\mathcal{F}_i(t,x), \mathcal{V}_i^+(t,x)$ and $\mathcal{V}_i^-(t,x)$ are nonnegative and continuous on $\mathbb{R} \times \mathbb{R}_+^n$ and continuously differential with respect to x.

(E2) There is a real number $T > 0$ such that for each $1 \leq i \leq n$, the functions $\mathcal{F}_i(t,x), \mathcal{V}_i^+(t,x)$ and $\mathcal{V}_i^-(t,x)$ are T-periodic in t.

(E3) If $x_i = 0$, then $\mathcal{V}_i^- = 0$. In particular, if $x \in X_s$, then $\mathcal{V}_i^- = 0$ for $i = 1,\ldots,m$.

(E4) $\mathcal{F}_i = 0$ for $i > m$.

(E5) If $x \in X_s$, then $\mathcal{F}_i(t,x) = \mathcal{V}_i(t,x) = 0$ for $i = 1,\ldots,m$.

(E6) $\rho(\Phi_M(T)) < 1$, where $\rho(\Phi_M(T))$ is the spectrum radius of $\Phi_M(T)$.

(E7) $\rho(\Phi_{-V(T)}) < 1$.

Then

$$D_x\mathcal{F}(t,x^0(t)) = \begin{pmatrix} F(t) & 0 \\ 0 & 0 \end{pmatrix}, \quad D_x\mathcal{V}(t,x^0(t)) = \begin{pmatrix} V(t) & 0 \\ J(t) & -M(t) \end{pmatrix},$$

where $J(t)$ is an $(n-m)\times m$ matrix.

Let $Y(t,s), t>s$, be the evolution operator of the linear T-periodic system

$$\frac{dy}{dt} = -V(t)y.$$

That is, for each $s \in \mathbb{R}$, the $m\times m$ matrix $Y(t,s)$ satisfies

$$\frac{d}{dt}Y(t,s) = -V(t)Y(t,s), \forall t > s, Y(s,s) = I,$$

where I is the $m\times m$ identity matrix. Set C_T be the ordered Banach space of all T-periodic functions from $\mathbb{R}$ to $\mathbb{R}^m$, which is equipped with the maximum norm and the positive cone $C_T^+ := \{\phi \in C_T : \phi(t) \geq 0, \forall t \geq 0\}$. Then we can define a linear operator $L : C_T \to C_T$ by

$$L(\phi)(t) = \int_0^\infty Y(t,t-a)F(t-a)\phi(t-a)da, \forall t \in \mathbb{R}, \phi \in C_T.$$

According to [3, 59], we call L the next infection operator, and define the spectral radius of L as the basic reproduction ratio

$$R_0 := \rho(L)$$

for the periodic epidemic model (1.7).

The following result shows that R_0 is a threshold parameter for the local stability of a disease-free periodic solution $x^0(t)$.

Theorem 1.3.1. [59, THEOREM 2.2] *Assume that (E1)-(E7) hold. Then the following statements are valid:*

(1) $R_0 = 1$ *if and only if* $\rho(\Phi_{F-V}(T)) = 1$.

(2) $R_0 > 1$ *if and only if* $\rho(\Phi_{F-V}(T)) > 1$.

(3) $R_0 < 1$ *if and only if* $\rho(\Phi_{F-V}(T)) < 1$.

Thus, $x^0(t)$ *is asymptotically stable if* $R_0 < 1$, *and unstable if* $R_0 > 1$.

Let $U(t, s, \lambda), t \geq s, s \in \mathbb{R}$, be the evolution operator of the following linear system

$$\frac{du}{dt} = [-V(t) + \frac{F(t)}{\lambda}]u, t \in \mathbb{R}.$$

Then the following result will be used in our numerical computation of R_0.

Theorem 1.3.2. [59, THEOREM 2.1] *Let (E1)-(E7) hold. Then the following statements are valid:*

(1) *If* $\rho(U(T, 0, \lambda)) = 1$ *has a positive solution* λ_0, *then* λ_0 *is an eigenvalue of* L, *and hence* $R_0 > 1$.

(2) *If* $R_0 > 1$, *then* $\lambda_0 = R_0$ *is the unique solution of* $\rho(U(T, 0, \lambda)) = 1$.

(3) $R_0 = 0$ *if and only if* $\rho(U(T, 0, \lambda)) < 1$ *for all* $\lambda > 0$.

1.4 Chain transitive sets

Let X be a metric space with metric d, and $f : X \to X$ be a continuous map.

Definition 1.4.1. *Let* $A \subset X$ *be a nonempty, invariant set for* f. *We say* A *is internally chain transitive if for any* $a, b \in A$ *and any* $\epsilon > 0$, $t_0 > 0$, *there is a finite sequence* $\{x_1 = a, x_2, ..., x_{m-1}, x_m = b\}$ *with* $x_i \in A$ *and* $t_i \geq t_0$, $1 \leq i \leq m-1$, *such that* $d(f(x_i), x_{i+1}) < \epsilon$ *for all* $1 \leq i \leq m-1$.

Theorem 1.4.1. [20, LEMMA 2.3] *Let $f : X \to X$ be a continuous map. Then the omega (alpha) limit set of any precompact positive (negative) orbit is internally chain transitive.*

Recall that a nonempty invariant subset M (i.e.,$f(M) = M$) of X is said to be isolated for $f : X \to X$ if it is the maximal invariant set in some neighborhood of itself. The stable set of M is defined by $W^s(M) := \{x \in X : \lim_{n\to\infty} d(f^n(x), M) = 0\}$.

Theorem 1.4.2. [20, THEOREM 3.1] *Let A be an attractor and C a compact internally chain transitive set for $f : X \to X$. If $C \cap W^s(A) \neq \emptyset$, then $C \subset A$.*

Let A and B are two isolated invariant sets. Then the set A is said to be chained to B, denoted $A \to B$, if there exists a full orbit through $x \notin A \cup B$ such that $\omega(x) \subset B$ and $\alpha(x) \subset A$. A finite sequence $\{M_1, ..., M_k\}$ of invariant sets is called a chain if $M_1 \to M_2 \to ... \to M_k$. The chain is called a cycle if $M_k = M_1$.

Theorem 1.4.3. [20, THEOREM 3.2] *Assume that each fixed point of f is an isolated invariant set, and there is no cycle chain of fixed point of f. Then any compact internally chain transitive set is a fixed points of f.*

Chapter 2

Bistable Waves in Competitive Recursion Systems

2.1 Introduction

Population dispersal is a very important topic in spatial ecology. In order to consider the effects of a dispersal process on evolution dynamics, ordinary differential equations or difference equations with spatial structure are usually used. In this chapter, we consider the following discrete-time two species competition model:

$$\begin{aligned} p_{n+1}(x) &= \int_{\mathbb{R}} \frac{(1+r_1)p_n(x-y)}{1+r_1(p_n(x-y)+a_1q_n(x-y))}k_1(y)dy, \\ q_{n+1}(x) &= \int_{\mathbb{R}} \frac{(1+r_2)q_n(x-y)}{1+r_2(q_n(x-y)+a_2p_n(x-y))}k_2(y)dy, \end{aligned} \tag{2.1}$$

where $p_n(x)$ and $q_n(x)$ denote the population densities of two species at time n and position x, respectively; $k_i(y)$ represents the dispersal kernel of two species and $\int_{\mathbb{R}} k_i(y)dy = 1, \int_{\mathbb{R}} e^{\alpha y}k_i(y)dy < \infty$, for all $\alpha \in \mathbb{R}, i = 1, 2$. We assume that all parameters are positive constants and the kernel k_i has the symmetric property

$k_i(-y) = k_i(y)$, which implies that the dispersal is isotropic and that the growth and dispersal properties are the same at each point.

There have been extensive investigations on traveling wave solutions of monotone discrete-time recursion systems

$$u_{n+1} = Q[u_n], n \geq 0, \tag{2.2}$$

where $u_n(x) = (u_n^1(x), ..., u_n^k(x))$ is a vector-valued function on $\mathbb{R}$, and Q is a translation invariant and order-preserving operator with monostable or bistable structure. We refer to [7, 21, 34, 35, 62, 63] and references therein. It is well known that the change of variables

$$u_n = p_n, \;\; v_n = 1 - q_n$$

converts system (2.1) into the following cooperative system:

$$\begin{aligned} u_{n+1}(x) &= \int_{\mathbb{R}} \frac{(1+r_1)u_n(x-y)}{1 + r_1(u_n(x-y) + a_1(1 - v_n(x-y)))} k_1(y)dy, \\ v_{n+1}(x) &= \int_{\mathbb{R}} \frac{a_2 r_2 u_n(x-y) + v_n(x-y)}{1 + r_2((1 - v_n(x-y)) + a_2 u_n(x-y))} k_2(y)dy, \end{aligned} \tag{2.3}$$

which is order preserving with respect to the standard componentwise ordering in the relevant range $0 \leq u_n \leq 1, 0 \leq v_n \leq 1$. Note that system (2.1) has four possible constant equilibria: $(0,0), (0,1), (1,0)$, and (p^*, q^*), where

$$p^* = \frac{1-a_1}{1-a_1a_2}, \;\; q^* = \frac{1-a_2}{1-a_1a_2},$$

and hence, system (2.3) has four equilibria: $E^0 = (0,1)$, $E^1 = (0,0)$, $E^2 = (1,1)$, and $E^3 = (u^*, v^*)$, where $u^* = p^*, v^* = 1 - q^*$. It is easy to see that the positive coexistence equilibrium exists if and only if $(1-a_1)(1-a_2) > 0$, and otherwise it is biologically irrelevant.

For the spatially homogeneous system associated with (2.1):

$$
\begin{aligned}
p_{n+1} = & \frac{(1+r_1)p_n}{1+r_1(p_n+a_1q_n)}, \\
q_{n+1} = & \frac{(1+r_2)q_n}{1+r_2(q_n+a_2p_n)},
\end{aligned}
\tag{2.4}
$$

Cushing et al. gave a complete classification of its global dynamics (see [8, Lemma 3]). Weinberger, Lewis and Li [63] obtained sufficient conditions for the linear determinacy of spreading speed of system (2.2) with the monostable structure, and applied their results to system (2.1) in a companion paper [26]. Recently, Lin, Li and Ruan [30] established the existence of monostable traveling waves connecting unstable equilibrium (0,0) and stable equilibrium (p^*, q^*), and the spreading speed for system (2.1) with $a_1, a_2 \in (0, 1)$. If $a_1, a_2 \in (1, +\infty)$, we know from [8, Lemma 3] that the equilibrium (p^*, q^*) is a saddle, (0,1) and (1,0) are stable, and (0,0) is unstable for the spatially homogeneous system (2.4). Further, there exists a separatrix Γ such that all orbits of system (2.4) below Γ converge to (1,0), while all orbits of system (2.4) above Γ converge to (0,1). We are interested in the existence of bistable traveling waves connecting (0,1) and (1,0), and their global stability with phase shift. Clearly, it suffices to study traveling waves connecting E^1 to E^2 for system (2.3). In order to obtain bistable traveling waves, we appeal to the theory of bistable waves recently developed in [13] for monotone semiflows, which allow the existence of multiple intermediate unstable equilibria in between two stable ones. For the global stability of traveling waves, we use a dynamical system approach, as illustrated in [67, Theorem 10.2.1] and [65, Theorem 3.1].

The rest of this chapter is organized as follows. In section 2.2, we establish the existence of bistable traveling waves by verifying the abstract assumptions in [13]. In section 2.3, we use Theorem 1.1.2 and the method of upper and lower solutions to prove the global stability of traveling waves and their uniqueness up to translation. In section 2.4, we present some numerical simulations to illustrate our analytic results.

2.2 Existence of bistable waves

In this section, we establish the existence of bistable traveling waves for system (2.3). We start with some notations.

Let $\mathcal{C} := C(\mathbb{R}, \mathbb{R}^2)$ be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ equipped with the compact open topology and cone $\mathcal{C}_+ = \{(\psi_1, \psi_2) \in \mathcal{C} : \psi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$. For any $a, b, r \in \mathbb{R}^2$ with $a \leq b$ and $r \gg 0$, we define $\mathcal{C}_r := \{\psi \in \mathcal{C} : r \geq \psi \geq 0\}$ and $[a, b]_{\mathcal{C}} := \{\psi \in \mathcal{C} : b \geq \psi \geq a\}$.

Since we are interested in bistable traveling waves, throughout this chapter we assume that $a_1 > 1$ and $a_2 > 1$. It is easy to see that the existence of traveling waves connecting two stable equilibria (0,1) and (1,0) in system (2.1) is equivalent to that of traveling waves connecting two ordered stable equilibria E^1 and E^2 in system (2.3). Further, there are two unordered unstable equilibria E^0 and E^3 between these two stable ones.

Define an operator $Q = (Q_1, Q_2)$ on $\mathcal{C}$ by

$$Q_1[u, v](x) = \int_{\mathbb{R}} \frac{(1 + r_1)u(x - y)}{1 + r_1(u(x - y) + a_1(1 - v(x - y)))} k_1(y)dy,$$

$$Q_2[u, v](x) = \int_{\mathbb{R}} \frac{a_2 r_2 u(x - y) + v(x - y)}{1 + r_2((1 - v(x - y)) + a_2 u(x - y))} k_2(y)dy.$$

Then system (2.3) can be expressed as

$$U_{n+1}(x) = Q[U_n](x), \ U_n := (u_n, v_n), \ n \geq 0.$$

Lemma 2.2.1. *The map Q satisfies (C1)-(C6) in Theorem 1.2.6 with $\beta = E^2$ and $E = \{E^0, E^1, E^2, E^3\}$.*

Proof. It is easy to verify Q satisfies (C1)-(C4). It remains to prove (C5) and (C6).

Let $\widehat{Q}$ be the restriction of Q to $[0, \beta]$, that is, $\widehat{Q} = (\widehat{Q}_1, \widehat{Q}_2)$ and

$$\widehat{Q}_1[u, v] = \frac{(1 + r_1)u}{1 + r_1(u + a_1(1 - v))},$$

$$\widehat{Q}_2[u, v] = \frac{a_2 r_2 u + v}{1 + r_2((1 - v) + a_2 u)}.$$

Then $\widehat{Q}$ has four fixed points $E^i, i = 0, 1, 2, 3$, and we need to show that the fixed point $E^1 = (0, 0)$ is stable from above and $E^2 = (1, 1)$ is stable from below. The Jacobian matrices of $\widehat{Q}$ at E^1 and E^2 are

$$J_{E^1} = \begin{pmatrix} \frac{1+r_1}{1+a_1 r_1} & 0 \\ \frac{a_2 r_2}{1+r_2} & \frac{1}{1+r_2} \end{pmatrix}, \quad J_{E^2} = \begin{pmatrix} \frac{1}{1+r_1} & \frac{a_1 r_1}{1+r_1} \\ 0 & \frac{1+r_2}{1+a_2 r_2} \end{pmatrix}.$$

It is obvious that J_{E^1} has two positive eigenvalues $\lambda_1 = \frac{1+r_1}{1+a_1 r_1} < 1$ and $\lambda_2 = \frac{1}{1+r_2} < 1$. If $\lambda_1 > \lambda_2$, then J_{E^1} has a unit eigenvector $e_0 \gg 0$ associated with λ_1 such that

$$J_{E^1}(e_0) = \lambda_1 e_0 \ll e_0;$$

If $\lambda_1 \leq \lambda_2 < 1$, we take $k \in (\lambda_2, 1), \varepsilon_0 \in \left(0, \frac{(k-\lambda_2)(1+r_2)}{a_2 r_2}\right)$ and unit vector $e_0 = \left(\frac{\varepsilon_0}{\sqrt{1+\varepsilon_0^2}}, \frac{1}{\sqrt{1+\varepsilon_0^2}}\right)^T \gg 0$ such that

$$J_{E^1}(e_0) \ll k e_0 \ll e_0.$$

By the continuous differentiability of $\widehat{Q}$, it then follows that there exists $\delta > 0$ such that

$$\begin{aligned}\widehat{Q}(\eta e_0) =&\widehat{Q}(0) + \int_0^1 D\widehat{Q}(t\eta e_0)\eta e_0 dt\\ =&\eta \int_0^1 D\widehat{Q}(t\eta e_0)e_0 dt\\ \leq&\eta k e_0 \ll \eta e_0\end{aligned}$$

for all $\eta \in (0, \delta]$, and hence, E^1 is strongly stable from above for the map $\widehat{Q}$. A similar argument shows that E^2 is strongly stable from below.

In order to calculate the spreading speed $c^*(E^0, E^1)$, we only need to consider the following one-dimensional monotone subsystem of (2.1):

$$q_{n+1}(x) = \int_{\mathbb{R}} \frac{(1+r_2)q_n(x-y)}{1+r_2 q_n(x-y)} k_2(y)\,dy,\ \ n \geq 0. \tag{2.5}$$

Let $h(q) = \frac{(1+r_2)q}{1+r_2 q}, \forall q \in [0,1]$. Then h satisfies the following two conditions:

(H1) $h \in C\left([0,1],[0,1]\right), h(0) = 0, h'(0) = 1 + r_2 > 1, h(1) = 1$, and $|h(q_1) - h(q_2)| < (1+r_2)|q_1 - q_2|, \forall q_1, q_2 \in [0,1]$.

(H2) $q < h(q) < h'(0)q, \forall q \in (0,1)$, and $h'(q) = \frac{1+r_2}{(1+r_2 q)^2} > 0, \forall q \in [0,1]$.

By [21, Theorem 2.1], (2.5) has a monostable traveling wave connecting 0 to 1 with the minimal wave speed c_h^*, where

$$c_h^* = \inf_{\mu>0} \frac{\ln(h'(0)\int_{\mathbb{R}} e^{\mu y} k_2(y)dy)}{\mu} = \inf_{\mu>0} \frac{\ln((1+r_2)\int_{\mathbb{R}} e^{\mu y} k_2(y)dy)}{\mu}$$

is the spreading speed, and $c^*(E^0, E^1) = c_h^*$.

For the computation of $c^*(E^0, E^2)$, we consider the following one-dimensional monotone system

$$p_{n+1}(x) = \int_{\mathbb{R}} \frac{(1+r_1)p_n(x-y)}{1+r_1p_n(x-y)} k_1(y)\, dy,\; n \geq 0. \tag{2.6}$$

Using the similar analysis as we did for system (2.5), we get

$$c^*(E^0, E^2) = \inf_{\mu>0} \frac{\ln((1+r_1)\int_{\mathbb{R}} e^{\mu y} k_1(y) dy)}{\mu}.$$

Further, we have the following claim.

Claim 2.2.1. $c^*(E^0, E^1) + c^*(E^0, E^2) > 0$.

Since $k_i(-y) = k_i(y), \forall y \in \mathbb{R}$, i=1,2, we have

$$\begin{aligned} K_i(\mu) :=& \int_{-\infty}^{\infty} e^{\mu y} k_i(y) dy = \int_{-\infty}^{\infty} e^{-\mu y} k_i(y) dy \\ =& \frac{1}{2} \int_{-\infty}^{\infty} (e^{\mu y} + e^{-\mu y}) k_i(y) dy \\ >& \int_{-\infty}^{\infty} k_i(y) dy = 1, \end{aligned}$$

and hence,

$$\ln((1+r_i) \int_{\mathbb{R}} e^{\mu y} k_i(y) dy) > 0.$$

Thus, we obtain

$$\lim_{\mu \to 0+} \frac{\ln((1+r_i)\int_{\mathbb{R}} e^{\mu y} k_i(y) dy)}{\mu} = \infty.$$

On the other hand, since $\int_{-\infty}^{\infty} k_i(y) dy = 2\int_0^{\infty} k_i(y) dy = 1$, there exists a sufficiently small number $y_0 > 0$ such that $\int_{y_0}^{\infty} k_i(y) dy > 0$, and

$$\int_{-\infty}^{\infty} e^{\mu y} k_i(y) dy \geq \int_{y_0}^{+\infty} e^{\mu y} k_i(y) dy \geq e^{\mu y_0} \int_{y_0}^{+\infty} k_i(y) dy.$$

By L'Hôspital's rule, we have

$$\liminf_{\mu\to\infty}\frac{\ln((1+r_i)\int_{\mathbb{R}} e^{\mu y}k_i(y)dy)}{\mu} \geq \lim_{\mu\to\infty}\frac{\ln((1+r_i)e^{\mu y_0}\int_{y_0}^{\infty} k_i(y)dy)}{\mu} = y_0 > 0.$$

Therefore,

$$c^*(E^0, E^i) = \inf_{\mu>0}\frac{\ln((1+r_i)\int_{\mathbb{R}} e^{\mu y}k_i(y)dy)}{\mu} > 0, i = 1, 2,$$

and hence, $c^*(E^0, E^1) + c^*(E^0, E^2) > 0$.

For the computation of $c^*(E^3, E^2)$, we let $x_n = u_n - u^*$ and $y_n = v_n - v^*$, then system (2.3) becomes

$$\begin{aligned} x_{n+1}(x) &= -u^* + \int_{\mathbb{R}} \frac{(1+r_1)(u^*+x_n(x-y))}{1+r_1(u^*+x_n(x-y))+a_1r_1(1-(v^*+y_n(x-y)))}k_1(y)dy, \\ y_{n+1}(x) &= -v^* + \int_{\mathbb{R}} \frac{a_2r_2(u^*+x_n(x-y))+v^*+y_n(x-y)}{1+r_2(1-(v^*+y_n(x-y)))+a_2r_2(u^*+x_n(x-y))}k_2(y)dy. \end{aligned} \tag{2.7}$$

It is easy to verify that system (2.7) is cooperative and positively invariant in $\mathcal{C}_\beta$, $\beta = (1-u^*, 1-v^*) \gg 0$. The spatially homogeneous system

$$\begin{aligned} x_{n+1} &= -u^* + \frac{(1+r_1)(u^*+x_n)}{1+r_1(u^*+x_n)+a_1r_1(1-(v^*+y_n))}, \\ y_{n+1} &= -v^* + \frac{a_2r_2(u^*+x_n)+v^*+y_n}{1+r_2(1-(v^*+y_n))+a_2r_2(u^*+x_n)}, \end{aligned} \tag{2.8}$$

has stable equilibrium 0 and unstable one β in $[0, \beta] \subset \mathbb{R}^2$, and there are no other equilibria between these two equilibria.

In order to compute the spreading speed $c^*(0, \beta)$ of system (2.7), we consider the linearization of (2.7) at zero solution

$$\begin{aligned} x_{n+1}(x) &= \int_{\mathbb{R}} \left(\frac{1 + a_1 r_1 (1 - v^*)}{1 + r_1} x_n(x - y) + \frac{a_1 r_1 u^*}{1 + r_1} y_n(x - y) \right) k_1(y) dy, \\ y_{n+1}(x) &= \int_{\mathbb{R}} \left(\frac{a_2 r_2 (1 - v^*)}{1 + r_2} x_n(x - y) + \frac{1 + r_2 v^*}{1 + r_2} y_n(x - y) \right) k_2(y) dy. \end{aligned} \tag{2.9}$$

For any $\mu \in \mathbb{R}_+$, let $x_n(x) = e^{-\mu x}\beta_n$, $y_n(x) = e^{-\mu x}\gamma_n, n \geq 0$. Then β_n, γ_n satisfy

$$\begin{aligned} \beta_{n+1} &= \frac{1 + a_1 r_1 (1 - v^*)}{1 + r_1} K_1(\mu)\beta_n + \frac{a_1 r_1 u^*}{1 + r_1} K_2(\mu)\gamma_n, \\ \gamma_{n+1} &= \frac{a_2 r_2 (1 - v^*)}{1 + r_2} K_1(\mu)\beta_n + \frac{1 + r_2 v^*}{1 + r_2} K_2(\mu)\gamma_n. \end{aligned} \tag{2.10}$$

Define the matrix

$$B_\mu := \begin{pmatrix} \frac{1+a_1 r_1 (1-v^*)}{1+r_1} K_1(\mu) & \frac{a_1 r_1 u^*}{1+r_1} K_2(\mu) \\ \frac{a_2 r_2 (1-v^*)}{1+r_2} K_1(\mu) & \frac{1+r_2 v^*}{1+r_2} K_2(\mu) \end{pmatrix}.$$

It is easy to see B_μ is positive for any $\mu \geq 0$, that is, each entry of B_μ is positive. Let $\lambda(\mu)$ be the principle eigenvalue of B_μ, then $\lambda(\mu)$ is positive with a strongly positive eigenvector (see [53, Theorem A.4]). In particular,

$$B_0 = \begin{pmatrix} \frac{1+a_1 r_1 (1-v^*)}{1+r_1} & \frac{a_1 r_1 u^*}{1+r_1} \\ \frac{a_2 r_2 (1-v^*)}{1+r_2} & \frac{1+r_2 v^*}{1+r_2} \end{pmatrix}.$$

Simple calculation can show that B_0 is to be the Jacobian matrix of $\widetilde{Q}$ evaluated at 0. From the unstability of 0, we know that $\lambda(0) > 1$. Since $K_i(\mu) > 1, \forall \mu > 0, i = 1, 2$, we have $B_\mu > B_0, \forall \mu > 0$. From the monotonicity of the principal eigenvalue with respect to the positive matrix [53, Theorem A.4], we know $\lambda(\mu) > \lambda(0) > 1, \forall \mu > 0$.

Let $\Phi(\mu) := \frac{\ln\lambda(\mu)}{\mu}$, then $\Phi(\mu) > 0, \forall\mu > 0$ and $\lim\limits_{\mu\to 0^+}\Phi(\mu) = \infty$. Further, we have

$$\begin{aligned}
\liminf_{\mu\to\infty}\Phi(\mu) =&\liminf_{\mu\to\infty}\frac{\ln\lambda(\mu)}{\mu}\\
=&\liminf_{\mu\to\infty}\frac{\ln\frac{\mathrm{tr}B_\mu+\sqrt{(\mathrm{tr}B_\mu)^2-4\det B_\mu}}{2}}{\mu}\\
\geq&\liminf_{\mu\to\infty}\frac{\ln(\mathrm{tr}B_\mu)}{\mu}\\
\geq&\liminf_{\mu\to\infty}\frac{\ln\frac{1+a_1r_1(1-v^*)}{1+r_1}K_1(\mu)}{\mu}\\
\geq&\lim_{\mu\to\infty}\frac{\ln\frac{1+a_1r_1(1-v^*)}{1+r_1}e^{\mu y_0}\int_{y_0}^{\infty}k_1(y)dy}{\mu}\\
=&y_0>0,
\end{aligned}$$

where $\mathrm{tr}B_\mu$ is the trace of B_μ. It follows that $\bar{c} := \inf\limits_{\mu>0}\Phi(\mu) > 0$.

Let operator $\widetilde{Q}$ and M from $\mathcal{C}_\beta$ to $\mathcal{C}_\beta$ be defined by the the right-hand side of systems (2.7) and (2.9), respectively. Since B_μ is positive, for any $\epsilon \in (0,1)$, we can choose $\vec{\delta} := (\delta,\delta)^T \gg 0$ in $\mathbb{R}^2$ sufficiently small such that

$$\widetilde{Q}[\psi] \geq (1-\epsilon)M[\psi],\ \ \forall\psi\in\mathcal{C}_{[0,\vec{\delta}]}.$$

Let $M_\epsilon = (1-\epsilon)M$. Then M_ϵ is monotonic and satisfying $Q \geq M_\epsilon$, and $M_\epsilon \to M$ as $\epsilon \to 0$. By [28, Theorem 3.10], we know $c^*(0,\beta) \geq \bar{c}$. Then we have $c^*(E^3,E^2) = c^*(0,\beta) \geq \bar{c} > 0$.

In order to computer $c^*(E^3,E^1)$, let $x_n = -u_n + u^*$, $y_n = -v_n + v^*$. Then system

(2.3) becomes

$$\begin{aligned}
x_{n+1}(x) =& u^* - \int_{\mathbb{R}} \frac{(1+r_1)(u^* - x_n(x-y))}{1 + r_1(u^* - x_n(x-y)) + a_1 r_1(1 - (v^* - y_n(x-y)))} k_1(y)dy, \\
y_{n+1}(x) =& v^* - \int_{\mathbb{R}} \frac{a_2 r_2(u^* - x_n(x-y)) + v^* - y_n(x-y)}{1 + r_2(1 - (v^* - y_n(x-y))) + a_2 r_2(u^* - x_n(x-y))} k_2(y)dy.
\end{aligned} \tag{2.11}$$

It is easy to verify that system (2.11) is cooperative and the spatially homogeneous system has unstable equilibrium 0 and stable equilibrium $\eta = (u^*, v^*) \gg 0$ in $[0, \eta] \subset \mathbb{R}^2$. Using a similar linearization argument as we did for system (2.7), we get the spreading speed $c^*(0, \eta)$ of (2.11), and $c^*(E^3, E^1) = c^*(0, \eta) > 0$. Therefore, $c^*(E^3, E^2) + c^*(E^3, E^1) > 0$. $\square$

As a consequence of Lemma 2.2.1 and Theorem 1.2.6, we have the following result.

Theorem 2.2.1. *Let all parameters be positive and $a_1, a_2 \in (1, \infty)$. Then there exists $c \in \mathbb{R}$ such that the cooperative system (2.3), which is obtained by making substitution $u_n = p_n, v_n = 1 - q_n$ in model (2.1), has a nondecreasing traveling wave $\varphi(x - cn) \in \mathcal{C}_{E^2}$ with speed c and connecting two stable equilibria $E^1 = (0,0)$ and $E^2 = (1,1)$.*

2.3 Global stability

In this section, we determine the global stability and uniqueness of bistable traveling waves for system (2.3).

Let $\varphi(x - cn) = (\varphi_1(x - cn), \varphi_2(x - cn))$ be a nondecreasing traveling wave solution of (2.3) connecting E^1 to E^2. Letting $z = x - c(n+1)$, we transform (2.3) into the following system

$$\bar{U}_{n+1}(z) = T_{-c} \circ Q[\bar{U}_n](z), \quad n \geq 0. \tag{2.12}$$

Thus, $\varphi(z)$ is an equilibrium solution of system (2.12), that is, $\varphi(z) = T_{-c} \circ Q[\varphi](z), \forall z \in \mathbb{R}$. In what follows, we denote $\bar{U}_n(z, \psi)$ to be the solution of (2.12) with initial data $\bar{U}_0 = \psi$. Clearly, the solution $U_n(x, \psi)$ of (2.3) with initial data ψ is given by $U_n(x, \psi) = \bar{U}_n(x - cn, \psi)$. Then we have the following observation.

Lemma 2.3.1. *The following statements are valid:*

(i) If $\psi \in [E^1, E^2]_C$ is nondecreasing and satisfies

$$\lim_{\xi \to -\infty} \psi(\xi) \ll E^3 \ll \lim_{\xi \to \infty} \psi(\xi), \tag{2.13}$$

then for any $\varepsilon > 0$, there exists $\tilde{z} = \tilde{z}(\varepsilon, \psi) > 0$ such that $\varphi(z - \tilde{z}) - \vec{\varepsilon} \leq \bar{U}_0(z, \psi) \leq \varphi(z + \tilde{z}) + \vec{\varepsilon}$.

(ii) If the kernel $k_i, i = 1, 2$, has a compact support, then for any $\varepsilon > 0$ and $\psi \in [E^1, E^2]_C$ with

$$\limsup_{\xi \to -\infty} \psi(\xi) \ll E^3 \ll \liminf_{\xi \to \infty} \psi(\xi), \tag{2.14}$$

there exist $\tilde{z} = \tilde{z}(\varepsilon, \psi) > 0$ and a large time $n_0 \in \mathbb{N}^+$ such that $\varphi(z - \tilde{z}) - \vec{\varepsilon} \leq \bar{U}_{n_0}(z, \psi) \leq \varphi(z + \tilde{z}) + \vec{\varepsilon}$.

Proof. (i) It is easy to see that

$$\limsup_{\xi \to -\infty} \psi(\xi) \ll E^1 + \vec{\varepsilon} = \lim_{\xi \to -\infty} \varphi(\xi) + \vec{\varepsilon},$$

$$\limsup_{\xi \to \infty} \psi(\xi) \ll E^2 + \vec{\varepsilon} = \lim_{\xi \to \infty} \varphi(\xi) + \vec{\varepsilon},$$

$$\liminf_{\xi \to -\infty} \psi(\xi) \gg E^1 - \vec{\varepsilon} = \lim_{\xi \to -\infty} \varphi(\xi) - \vec{\varepsilon},$$

$$\liminf_{\xi \to \infty} \psi(\xi) \gg E^2 - \vec{\varepsilon} = \lim_{\xi \to \infty} \varphi(\xi) - \vec{\varepsilon}.$$

Then there exists $Z_0 > 0$ such that $\varphi(z) - \vec{\varepsilon} \leq \psi(z) \leq \varphi(z) + \vec{\varepsilon}$ holds for all $|z| \geq Z_0$.

By the monotonicity of ψ and φ, there exists $\tilde{z} > 0$ such that $\varphi(z-\tilde{z})-\bar{\varepsilon} \leq \bar{U}_0(z,\psi) \leq \varphi(z+\tilde{z})+\bar{\varepsilon}$.

(ii) Let $L > 0$ be a sufficiently large number such that supp$k_i \subseteq [-L, L], i = 1, 2$, and $\limsup\limits_{\xi \to -\infty} \psi(\xi) \ll E^3 \ll \liminf\limits_{\xi \to \infty} \psi(\xi)$. Without loss of generality, we assume $\psi(\xi) \leq l_1, \forall \xi \in \mathbb{R}$, and $\psi(\xi) \leq l_2, \forall \xi \leq 0$, where $E^3 \ll l_1 \leq E^2, E^1 \leq l_2 \ll E^3$. Let $V_n^+ = \bar{U}_n(2l_1 - l_2), V_n^- = \bar{U}_n(l_2)$ be the spatially homogeneous solutions of (2.12) with $V_0^+ = 2l_1 - l_2$ and $V_0^- = l_2$. Let $\bar{c} \in (c-L, c+L)$ and $\xi : \mathbb{R} \to [0,1]$ be a nondecreasing functional satisfying $\xi(z) \equiv 1, \forall z \geq 1$, and $\xi(z) \equiv 0, \forall z \leq 0$. Define

$$V_n(z) = V_n^+ \xi(z + n\bar{c}) + V_n^-(1 - \xi(z + n\bar{c})).$$

Then it is easy to verify $V_0(z) \geq \psi(z), \forall z \in \mathbb{R}$. We now claim that for any discrete time n, there exist $\tilde{z}_n \in \mathbb{R}$ such that

$$V_{n+1}(z) \geq Q[V_n](z - \tilde{z}_{n+1} + c), \ \forall z \in \mathbb{R}.$$

We first prove that

$$V_{n+1}(z) \geq Q[V_n](z + c)$$

whenever $|z|$ is large enough.

For the sake of convenience, we define the nondecreasing operator $G = (G_1, G_2) : \mathbb{R}^2 \to \mathbb{R}^2$ as

$$G_1(x_1, x_2) = \frac{(1+r_1)x_1}{1 + a_1 r_1 + r_1 x_1 - a_1 r_1 x_2}, \quad G_2(x_1, x_2) = \frac{a_2 r_2 x_1 + x_2}{1 + r_2 + a_2 r_2 x_1 - r_2 x_2}.$$

Then system (2.12) can be expressed as

$$\bar{U}_{n+1}(z) = \int_{\mathbb{R}} G(\bar{U}_n(z + c - y))S(y)dy, \ \ n \geq 0, \tag{2.15}$$

where $S(y) = \text{diag}(k_1(y), k_2(y))$.

For fixed $n \in \mathbb{N}^+$, if $z > -n\bar{c} - c + L + 1$, then $z + (n+1)\bar{c} > z + n\bar{c} + c - L > 1$, and

$$\begin{aligned}
&V_{n+1}(z) - Q[V_n](z+c) \\
=&V_{n+1}^+\xi(z+(n+1)\bar{c}) + V_{n+1}^-(1-\xi(z+(n+1)\bar{c})) \\
&- \int_{-L}^{L} G(V_n^+\xi(z+n\bar{c}+c-y) + V_n^-(1-\xi(z+n\bar{c}+c-y))S(y)dy \\
=&V_{n+1}^+ - \int_{-L}^{L} G(V_n^+)S(y)dy = 0.
\end{aligned}$$

If $z < -n\bar{c} - c - L$, then $z + (n+1)\bar{c} < z + n\bar{c} + c + L < 0$. It follows that

$$\begin{aligned}
&V_{n+1}(z) - Q[V_n](z+c) \\
=&V_{n+1}^+\xi(z+(n+1)\bar{c}) + V_{n+1}^-(1-\xi(z+(n+1)\bar{c})) \\
&- \int_{-L}^{L} G(V_n^+\xi(z+n\bar{c}+c-y) + V_n^-(1-\xi(z+n\bar{c}+c-y))S(y)dy \\
=&V_{n+1}^- - \int_{-L}^{L} G(V_n^-)S(y)dy = 0.
\end{aligned}$$

Consequently, the above claim follows from the fact that $V_{n+1}(\cdot)$ and $Q[V_n](\cdot + c)$ are increasing due to the monotonicity of operator Q and $V_n(\cdot)$.

Since $V_0(z) \geq \psi(z), \forall z \in \mathbb{R}$, combining the claim we have

$$\begin{aligned}
V_1(z) \geq & Q[V_0](z - \tilde{z}_1 + c) \geq Q[\psi](z - \tilde{z}_1 + c) = \bar{U}_1(z - \tilde{z}_1, \psi), \\
V_2(z) \geq & Q[V_1](z - \tilde{z}_2 + c) \geq Q[\bar{U}_1](z - \tilde{z}_1 - \tilde{z}_2 + c) = \bar{U}_2(z - \tilde{z}_1 - \tilde{z}_2, \psi).
\end{aligned}$$

By induction, we have

$$V_n(z) \geq \bar{U}_n(z - \tilde{z}_1 - \tilde{z}_2 - \ldots - \tilde{z}_n, \psi),\ n \geq 0.$$

Note that $\lim_{z\to-\infty} V_n(z) = V_n^-$, $\lim_{z\to\infty} V_n(z) = V_n^+$, $\lim_{n\to\infty} V_n^- = E^1$, and $\lim_{n\to\infty} V_n^+ = E^2$. It then follows that for any $\varepsilon > 0$, there exists $N_0 \in \mathbb{N}^+$ such that

$$\lim_{z\to-\infty} V_{\tilde{n}}(z) = V_{\tilde{n}}^- \leq E^1 + \frac{\vec{\varepsilon}}{2} \ll E^1 + \vec{\varepsilon} = \lim_{z\to-\infty} \varphi(z) + \vec{\varepsilon},\ \forall\, \tilde{n} \geq N_0,$$

$$\lim_{z\to\infty} V_{\tilde{n}}(z) = V_{\tilde{n}}^+ \leq E^2 + \frac{\vec{\varepsilon}}{2} \ll E^2 + \vec{\varepsilon} = \lim_{z\to\infty} \varphi(z) + \vec{\varepsilon},\ \ \forall\, \tilde{n} \geq N_0.$$

Thus, there exists $Z_1 > 0$ such that

$$V_{\tilde{n}}(z) \leq \varphi(z) + \vec{\varepsilon},\ \ \forall\, |z| \geq Z_1.$$

By the monotonicity of $V_{\tilde{n}}(\cdot)$ and $\varphi(\cdot)$, there exists $\tilde{z}_0 \in \mathbb{R}$ such that

$$V_{\tilde{n}(z)} \leq \varphi(z + \tilde{z}_0) + \vec{\varepsilon},\ \forall z \in \mathbb{R}.$$

Hence, we have

$$\bar{U}_{\tilde{n}}(z - \tilde{z}_1 - \tilde{z}_2 - \ldots - \tilde{z}_n, \psi) \leq V_{\tilde{n}}(z) \leq \varphi(z + \tilde{z}_0) + \vec{\varepsilon},\ \forall z \in \mathbb{R}.$$

Let $\tilde{z} = \Sigma_{i=0}^{\tilde{n}} \tilde{z}_i$. It then follows that

$$\bar{U}_{\tilde{n}}(z, \psi) \leq \varphi(z + \tilde{z}) + \vec{\varepsilon},\ \forall z \in \mathbb{R}.$$

A similar argument on the lower bound of $U_{\tilde{n}}(z, \psi)$ completes the proof. □

In order to use the method of upper and lower solutions, we first introduce the following concepts.

Definition 2.3.1. *A function sequence $W_n^+(z) \in C(\mathbb{R}, \mathbb{R}^2), n \geq 0$, is an upper solution* *of* (2.12) *if* $W_n^+(z)$ *satisfies*

$$W_{n+1}^+ \geq Q[W_n^+](z+c), \quad n \geq 0.$$

A function sequence $W_n^-(z) \in C(\mathbb{R}, \mathbb{R}^2), n \geq 0$, *is a lower solution of* (2.12) *if* $W_n^-(z)$ *satisfies*

$$W_{n+1}^- \leq Q[W_n^-](z+c), \quad n \geq 0.$$

Note that the Fréchet derivatives of G at E^1 and E^2 are

$$DG(0,0) = \begin{pmatrix} \frac{1+r_1}{1+a_1r_1} & 0 \\ \frac{a_2r_2}{1+r_2} & \frac{1}{1+r_2} \end{pmatrix}, \quad DG(1,1) = \begin{pmatrix} \frac{1}{1+r_1} & \frac{a_1r_1}{1+r_1} \\ 0 & \frac{1+r_2}{1+a_2r_2} \end{pmatrix}.$$

It is obvious that $DG(0,0)$ and $DG(1,1)$ are nonnegative with eigenvalues between 0 and 1. Choose $\epsilon_1 > 0$ small enough such that $DG(0,0) < A^-, DG(1,1) < A^+$, where

$$A^- = \begin{pmatrix} \frac{1+r_1}{1+a_1r_1} & \epsilon_1 \\ \frac{a_2r_2}{1+r_2} & \frac{1}{1+r_2} \end{pmatrix}, \quad A^+ = \begin{pmatrix} \frac{1}{1+r_1} & \frac{a_1r_1}{1+r_1} \\ \epsilon_1 & \frac{1+r_2}{1+a_2r_2} \end{pmatrix},$$

and the principle eigenvalues of $A^\pm$ are between 0 and 1. Since $A^\pm$ are positive, there exist strongly positive eigenvectors $\rho^\pm = (\rho_1^\pm, \rho_2^\pm)$ corresponding to the principle eigenvalues of $A^\pm$ satisfying $\vec{0} \ll \rho^- \leq \rho^+ \leq \vec{1}$. Note that we can choose $\rho^\pm$ as close to the origin as we wish due to the fact that the eigenvector space is linearly closed. Let $\rho(z) : \mathbb{R} \to \mathbb{R}^2$ be a positive nondecreasing map such that $\rho(z) = \rho^+, \forall z \geq z_1 > 0$, and $\rho(z) = \rho^-, \forall z \leq z_2 < 0$, where $z_i, i = 1, 2$, are two fixed real numbers. Motivated by [65], we have the following result on the upper and lower solutions for (2.3).

Lemma 2.3.2. *There exist positive number* σ *and* $\varepsilon_0 \in (0,1)$ *such that for any* $\hat{z}$ *and*

$\varepsilon \in (0, \varepsilon_0)$,

$$W_n^{\pm} = \varphi(z \pm \hat{z} \pm \varepsilon(1 - e^{-\sigma n})) \pm \varepsilon\rho(z \pm \hat{z})e^{-\sigma n}, \ \ \forall z \in \mathbb{R}, \ n \geq 0$$

are upper and lower solutions of system (2.12), *respectively.*

Proof. Without loss of generality, we assume that $\hat{z} = 0$. Let $z_n = \varepsilon(1 - e^{\sigma n})$, $\forall n \geq 0$. Then $\{z_n\}_{n\geq 0}$ is increasing and between 0 and 1, where the positive number σ is to be determined. Denote $D_n^{\pm}(z) := W_{n+1}^{\pm}(z) - Q[W_n^{\pm}](z + c)$, and $G_j^i(u) := \frac{\partial}{\partial x_j} G^i(u)$, $B = \sup\{|G_j^i(u)| : u \in [E^1 - \vec{1}, E^2 + \vec{1}]\}$, where $u = (x_1, x_2) \in \mathbb{R}^2$. It is obvious that there exist $\delta > 0, k \in (0, 1)$ such that $G_j^i(u) \leq A_{ij}^-$ for all $\|u - E^1\| \leq \delta$, $G_j^i(u) \leq A_{ij}^+$ for all $\|u - E^2\| \leq \delta$, and $A^{\pm}\rho \leq k\rho$ for all $\|\rho - \rho^{\pm}\| \leq \delta$, where $\rho := (\rho_1, \rho_2) \in \mathbb{R}^2$. Since $\varphi(-\infty) := \lim_{z\to-\infty} \varphi(z) = E^1, \varphi(\infty) := \lim_{z\to\infty} \varphi(z) = E^2$, and $\rho(z) \subseteq [\rho^-, \rho^+], \forall z \in \mathbb{R}$, it follows that there exist $M > \max\{z_1 + 1, 1 - z_2\}$ and $\varepsilon_1 \in (0, 1)$ such that

$$\|\varphi(z) + \varepsilon\rho(\eta) - E^1\| \leq \delta, \ \ \forall \varepsilon \in (0, \varepsilon_1], \ \ \eta \leq -M + 1, \ \ z \leq -M + 1,$$

$$\|\varphi(z) + \varepsilon\rho(\eta) - E^2\| \leq \delta, \ \ \forall \varepsilon \in (0, \varepsilon_1], \ \ \eta \geq M - 1, \ \ z \geq M - 1.$$

Then we have

$$
\begin{aligned}
&D_n^+(z) = W_{n+1}^+(z) - Q[W_n^+](z+c) \\
=&\varphi(z+z_{n+1}) + \varepsilon\rho(z)e^{-\sigma(n+1)} \\
&- \int_{\mathbb{R}} G(\varphi(z+z_n+c-y) + \varepsilon\rho(z+c-y)e^{-\sigma n})S(y)dy \\
=&\varphi(z+z_{n+1}) - \varphi(z+z_n) + \varepsilon\rho(z)e^{-\sigma(n+1)} \\
&- \int_{\mathbb{R}} [G(\varphi(z+z_n+c-y) + \varepsilon\rho(z+c-y)e^{-\sigma n}) - G(\varphi(z+z_n+c-y))]S(y)dy \\
=&\varphi(z+z_{n+1}) - \varphi(z+z_n) + \varepsilon\rho(z)e^{-\sigma(n+1)} \\
&- \int_{\mathbb{R}} [G(\varphi(y+z_n) + \varepsilon\rho(y)e^{-\sigma n}) - G(\varphi(y+z_n))]S(z+c-y)dy \\
=&\varphi(z+z_{n+1}) - \varphi(z+z_n) + \varepsilon\rho(z)e^{-\sigma(n+1)} \\
&- \int_{\mathbb{R}} \left(\int_0^1 DG(\varphi(y+z_n) + s\varepsilon\rho(y)e^{-\sigma n})\varepsilon\rho(y)e^{-\sigma n} ds \right) S(z+c-y)dy.
\end{aligned}
\tag{2.16}
$$

Let I be the 2×2 identity matrix and $\Gamma_n = [-M - z_n - \eta, M - z_n + \eta]$, where $\eta > 1$ is large enough such that

$$
\left(\int_{-\infty}^{-\eta+c} + \int_{\eta+c}^{\infty} \right) S(y)dy < \varepsilon I.
$$

Now for any $n \geq 0$, we claim $D_n^+(z) \geq 0$. We consider three cases.

Case (i): $z > M - z_n + \eta$. It is clear that $z > M - 1$ and $z + c - y \geq \eta + c$ if

$y \le M - z_n$. By the monotonicity of φ, we have

$$
\begin{aligned}
& D_n^+(z) \ge \varepsilon\rho(z)e^{-\sigma(n+1)} \\
& - \int_{\mathbb{R}} \left(\int_0^1 DG(\varphi(y+z_n) + s\varepsilon\rho(y)e^{-\sigma n})\varepsilon\rho(y)e^{-\sigma n} ds \right) S(z+c-y)dy \\
=& \varepsilon\rho(z)e^{-\sigma(n+1)} - \left(\int_{-\infty}^{-M-z_n} + \int_{-M-z_n}^{M-z_n} + \int_{M-z_n}^{\infty} \right) \\
& \left(\int_0^1 DG(\varphi(y+z_n) + s\varepsilon\rho(y)e^{-\sigma n})\varepsilon\rho(y)e^{-\sigma n} ds \right) S(z+c-y)dy \\
\ge& \varepsilon\rho(z)e^{-\sigma(n+1)} - \left(\int_{-\infty}^{-M-z_n} + \int_{M-z_n}^{\infty} \right) k\rho(y)\varepsilon e^{-\sigma n} S(z+c-y)dy \\
& - \int_{-M-z_n}^{M-z_n} \left(\int_0^1 DG(\varphi(y+z_n) + s\varepsilon\rho(y)e^{-\sigma n})\varepsilon\rho(y)e^{-\sigma n} ds \right) S(z+c-y)dy \\
\ge& \varepsilon\rho^+ e^{-\sigma(n+1)} - k\rho^+\varepsilon e^{-\sigma n}\varepsilon - k\rho^+\varepsilon e^{-\sigma n} - 2B\varepsilon\|\rho^+\| e^{-\sigma n}\varepsilon\vec{e} \\
=& \varepsilon e^{-\sigma n}(\rho^+(e^{-\sigma} - k) - k\rho^+\varepsilon - 2B\|\rho^+\|\varepsilon\vec{e}) \ge 0
\end{aligned}
$$

provided $\sigma \in (0, -\ln k)$, and ε is small enough.

Case(ii): $z < -M - z_n - \eta$. Clearly, $z < -M + 1$, and $z + c - y < -\eta + c$ if $y > -M - z_n$. Then

$$
\begin{aligned}
& D_n^+(z) \ge \varepsilon\rho(z)e^{-\sigma(n+1)} - \left(\int_{-\infty}^{-M-z_n} + \int_{M-z_n}^{\infty} \right) k\rho(y)\varepsilon e^{-\sigma n} S(z+c-y)dy \\
& - \int_{-M-z_n}^{M-z_n} \left(\int_0^1 DG(\varphi(y+z_n) + s\varepsilon\rho(y)e^{-\sigma n})\varepsilon\rho(y)e^{-\sigma n} ds \right) S(z+c-y)dy \\
\ge& \varepsilon\rho^- e^{-\sigma(n+1)} - \int_{-\infty}^{-M-z_n} k\rho(y)\varepsilon e^{-\sigma n} S(z+c-y)dy \\
& - k\varepsilon e^{-\sigma n}\rho^+\varepsilon - 2B\varepsilon\|\rho^+\| e^{-\sigma n}\varepsilon\vec{e} \\
\ge& \varepsilon\rho^- e^{-\sigma(n+1)} - k\rho^-\varepsilon e^{-\sigma n} - k\varepsilon e^{-\sigma n}\rho^+\varepsilon - 2B\varepsilon\|\rho^+\| e^{-\sigma n}\varepsilon\vec{e} \\
=& \varepsilon e^{-\sigma n}(\rho^-(e^{-\sigma} - k) - k\rho^+\varepsilon - 2B\|\rho^+\|\varepsilon\vec{e}) \ge 0,
\end{aligned}
$$

provided that $\sigma \in (0, -\ln k)$, and ε is small enough.

Case(iii): $z \in \Gamma_n = [-M - z_n - \eta, M - z_n + \eta]$, that is, $z + z_n \in [-M - \eta, M + \eta]$.

The uniform continuity of φ and [34, Lemma 5] imply that $\varphi \in C^1(\mathbb{R}, \mathbb{R}^2)$, $\varphi'(z)$ is uniformly continuous, and

$$\varphi'(z) = \int_{\mathbb{R}} DG(\varphi(y))\varphi'(y)S(z+c-y)dy \gg 0.$$

Since φ is strictly increasing in compact set $[-M-2\eta, M+2\eta]$, there exists $\vec{\theta} = (\theta, \theta) \gg 0$ such that

$$\varphi(y) - \varphi(x) \geq \vec{\theta}(y-x), \ y > x, \ \forall x, y \in [-M-2\eta, M+2\eta]. \tag{2.17}$$

It is obvious that

$$0 < d_n = (z + z_{n+1}) - (z + z_n) = z_{n+1} - z_n = \varepsilon e^{-\sigma n}(1 - e^{-\sigma}) < 1 < \eta,$$

and hence, $z + z_{n+1} < z + z_n + 1 < M + \eta + 1 < M + 2\eta$. By (2.17), we have

$$\varphi(z + z_{n+1}) - \varphi(z + z_n) \geq \vec{\theta}(z_{n+1} - z_n). \tag{2.18}$$

It follows from (2.16) and (2.18) that

$$\begin{aligned} D_n^+(z) \geq & \vec{\theta}(z_{n+1} - z_n) + \varepsilon\rho^- e^{-\sigma(n+1)} - 2B\rho^+ e^{-\sigma n}\varepsilon\vec{e} \\ = & \vec{\theta}\varepsilon e^{-\sigma n}(1 - e^{-\sigma}) + \varepsilon\rho^- e^{-\sigma(n+1)} - 2B\rho^+ e^{-\sigma n}\varepsilon\vec{e} \\ = & \varepsilon e^{-\sigma n}(\vec{\theta}(1 - e^{-\sigma}) + \rho^- e^{-\sigma} - 2B\|\rho^+\|\vec{e}) \geq 0, \end{aligned}$$

provided $\|\rho^+\| \leq \theta(1 - e^{-\sigma})/2B$.

Combining cases (i)-(iii), we see that there exist $\sigma > 0$, and sufficiently small number $\varepsilon_0 \in (0, 1)$ such that $D_n^+(z) \geq 0$, $n \geq 0$, $z \in \mathbb{R}$. Thus, $W_n^+(z)$ is an upper solution of system (2.12). By a similar argument, we can prove $W_n^-(z)$ is a lower solution of (2.12). □

Lemma 2.3.3. *The wave profile φ is a Lyapunov stable equilibrium of* (2.12).

Proof. Let ε_0 and $W_n^{\pm}(z)$ be given in Lemma 2.3.2 with $\hat{z} = 0$. By the uniform continuity of φ and the boundedness of $\rho(z)$, it follows that there exists $K > 0$, independent of ε, such that $\|W_n^{\pm}(z, \varepsilon) - \varphi(z)\| < K\varepsilon$, $\forall z \in \mathbb{R}$, $\varepsilon \in (0, \varepsilon_0)$. For any $\varepsilon \in (0, \varepsilon_0)$, let $\delta = \varepsilon \min\{\rho_1^-, \rho_2^-\} > 0$, then $\varepsilon\rho(z) \geq \vec{\delta}$. Thus, for any given ψ satisfying $\|\psi - \varphi\| < \delta$, we have

$$W_0^-(z, \varepsilon) = \varphi(z) - \varepsilon\rho(z) \leq \psi \leq \varphi(z) + \varepsilon\rho(z) = W_0^+(z, \varepsilon).$$

Then the comparison principle implies that

$$W_n^-(z, \varepsilon) \leq \bar{U}_n(z, \psi) \leq W_n^+(z, \varepsilon), \ \forall z \in \mathbb{R},$$

and hence, $\|\bar{U}_n(\cdot, \psi) - \varphi(\cdot)\| \leq K\varepsilon$, $n \geq 0$, which completes the proof. □

Let $\mathcal{X} = BUC(\mathbb{R}, \mathbb{R}^2)$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ with the usual supreme norm. Let $\mathcal{X}_+ = \{(\psi_1, \psi_2) \in \mathcal{X} : \psi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$. Then $\mathcal{X}_+$ is a closed cone of $\mathcal{X}$ and its induced partial ordering makes $\mathcal{X}$ into a Banach lattice.

Now we are in the position to prove the main result of this section.

Theorem 2.3.1. *Let $\varphi(x - cn)$ be a monotone traveling wave solution of system* (2.3) *and $U_n(x, \psi)$ be the solution of* (2.3) *with $U_0(\cdot, \psi) = \psi(\cdot) \in [E^1, E^2]_{\mathcal{X}}$. Then the following statements are valid:*

(i) For any nondecreasing $\psi \in [E^1, E^2]_{\mathcal{X}}$ satisfying (2.13), *there exists $s_\psi \in \mathbb{R}$ such that $\lim_{n\to\infty} \|U_n(x, t, \psi) - \varphi(x - cn + s_\psi)\| = 0$ uniformly for $x \in \mathbb{R}$, and*

any monotone traveling wave solution of system (2.3) *connecting* E^1 *to* E^2 *is a translation of* φ.

(ii) *If* $k_i, i = 1, 2$, *has a compact support, then for any* $\psi \in [E^1, E^2]_{\mathcal{X}}$ *satisfying* (2.14), *there exists* $s_\psi \in \mathbb{R}$ *such that* $\lim_{n\to\infty} \|U_n(x, t, \psi) - \varphi(x - cn + s_\psi)\| = 0$ *uniformly for* $x \in \mathbb{R}$, *and any traveling wave solution of system* (2.3) *connecting* E^1 *to* E^2 *is a translation of* φ.

Proof. Let $\varepsilon \in (0, \varepsilon_0)$ be given as in Lemma 2.3.2. From (i) and (ii) in Lemma 2.3.1, we see that for $\varepsilon\rho^- \gg 0$ and any $\psi \in [E^1, E^2]_{\mathcal{X}}$ satisfying (2.13) in case (i), or satisfying (2.14) in case (ii), there exist n_0 and $\tilde{z}$ such that for any $z \in \mathbb{R}$, we have

$$\bar{U}_{n_0}(z, \psi) \le \varphi(z + \tilde{z}) + \varepsilon\rho^- \le \varphi(z + \tilde{z}) + \varepsilon\rho(z + \tilde{z}) = W_0^+,$$

and

$$\bar{U}_{n_0}(z, \psi) \ge \varphi(z - \tilde{z}) - \varepsilon\rho^- \ge \varphi(z - \tilde{z}) - \varepsilon\rho(z - \tilde{z}) = W_0^-.$$

Then the comparison principle and the construction of $W_n^\pm(z)$ imply that

$$W_n^-(z) \le \bar{U}_n(z, \bar{U}_{n_0}(\cdot)) \le W_n^+(z), \forall z \in \mathbb{R}, n \in \mathbb{N}^+.$$

Since $\bar{U}_n(z, \bar{U}_{n_0}(\cdot)) = \bar{U}_{n+n_0}(z, \psi), \forall z \in \mathbb{R},\ n \in \mathbb{N}^+$, we have

$$\varphi(z - \tilde{z} - \varepsilon_0) - \varepsilon\rho(z - \tilde{z})e^{-\sigma n} \le \bar{U}_{n+n_0}(z, \psi) \le \varphi(z + \tilde{z} + \varepsilon_0) - \varepsilon\rho(z + \tilde{z})e^{-\sigma n}. \quad (2.19)$$

Let $\Phi_n(\psi) := \bar{U}_n(\cdot, \psi), \forall \psi \in \mathcal{X}, n \in \mathbb{N}^+$ be the solution semiflow determined by (2.12). By (2.19), the forward orbit $\gamma^+(\psi) := \{\Phi_n(\psi) : n \ge 0\}$ is bounded in $\mathcal{X}$. Note that $\lim_{z\to-\infty} \varphi(z) = E^1$, $\lim_{z\to\infty} \varphi(z) = E^2$. By Ascoli-Arzelà theorem, it then follows that $\gamma^+(\psi)$ is precompact in $\mathcal{X}$, and hence, the omega limit set $\omega(\psi)$ is nonempty, compact and invariant.

Let $z_0 = \tilde{z} + \varepsilon_0$, and $n \to \infty$ in (2.19), we have the omega limit set $\omega(\psi) \subset I := [\varphi(\cdot - z_0), \varphi(\cdot + z_0)]_{\mathcal{X}}$. Let $h(s) = \varphi(\cdot + s), \forall s \in [-z_0, z_0]$. Then h is a monotone homeomorphism from $[-z_0, z_0]$ onto a subset $\hat{I} \subset I$. Let $V = [E^1, E^2]_{\mathcal{X}}$. Then $\Phi_n : V \to V$ is a monotone autonomous semiflow. By Lemma 2.3.3, each $h(s)$ is a stable equilibrium for Φ_n. Clearly, each $\phi \in \hat{I}$ is increasing and satisfies (2.13) and (2.14), and hence, $\gamma^+(\phi)$ is precompact. By Theorem 1.1.2, it suffices to verify the condition (3a) to obtain the convergence of $\gamma^+(\psi)$.

Assume that for some $s_0 \in [-z_0, z_0)$, $\phi_0 \in \hat{I}$ and $\varphi(\cdot + s_0) <_{\mathcal{X}} \phi(\cdot)$ for all $\phi \in \omega(\phi_0)$, that is, $\varphi(\cdot + s_0) <_{\mathcal{X}} \omega(\phi_0)$. By the strong monotonicity of Q, we know $\varphi(z + s_0) \ll \Phi_n(\phi)(z)$, $\forall z \in \mathbb{R}$, $n \in \mathbb{N}$. By the invariance of $\omega(\phi_0)$, we get $\varphi(z + s_0) \ll \phi(z)$, $\forall \phi \in \omega(\phi_0)$, $z \in \mathbb{R}$.

By the uniform continuity of φ' and [56, Corollary A.19], it follows that $\lim_{z \to \infty} \varphi'(z) = \vec{0}$, and hence, we can choose a large positive number $z_1 \in (z_0, \infty)$ such that $\delta := \sup_{|z| \geq z_1 - z_0} \|\varphi'(z)\| \leq \frac{1}{4} \min\{\rho_1^-, \rho_2^-\}$. By the compactness of $\omega(\phi_0)$, there exists $s_1 \in (s_0, z_0)$ such that $s_1 - s_0 < \varepsilon_0$, and

$$\varphi(z + s_1) \ll \phi(z), \forall z \in [-z_1, z_1], \phi \in \omega(\phi_0).$$

For any fixed $\phi \in \omega(\phi_0)$, there exists a sequence $\{n_j\}$ such that $n_j \to \infty$ as $j \to \infty$, and $\lim_{j \to \infty} \Phi_{n_j}(\phi_0) = \phi$. Fix an n_j such that

$$\|\Phi_{n_j}(\phi_0) - \phi\| \leq \delta(s_1 - s_0).$$

Since $\varphi(z + s_1) \ll \phi(z)$, $\forall z \in [-z_1, z_1]$, and

$$\varphi(z + s_0) - \varphi(z + s_1) \ll \phi(z) - \varphi(z + s_1), \forall z \in \mathbb{R},$$

we have

$$\begin{aligned}\Phi_{n_j}(\phi_0)(z) - \varphi(z+s_1) =& \Phi_{n_j}(\phi_0)(z) - \phi(z) + \phi(z) - \varphi(z+s_1)\\ &\geq -(s_1 - s_0)\vec{\delta} - \sup_{|z|\geq z_1} \|\varphi(z+s_0) - \varphi(z+s_1)\|\vec{e}\\ &\geq -(s_1 - s_0)\vec{\delta} - (s_1 - s_0)\sup_{|z|\geq z_1}\|\varphi'(z)\|\vec{e}\\ &\geq -(s_1 - s_0)\vec{\delta} - (s_1 - s_0)\vec{\delta}\\ &= -2(s_1 - s_0)\vec{\delta}\\ &\geq -\varepsilon_1\rho(z+s_1).\end{aligned}$$

where $\varepsilon_1 = \frac{s_1 - s_0}{2} < \varepsilon_0$. By the construction of $W_n^-(z)$, we get

$$\Phi_{n_j}(\phi_0)(z) \geq \varphi(z+s_1) - \varepsilon_1\rho(z+s_1) = W_0^-(z).$$

It follows that

$$\begin{aligned}\Phi_n(\Phi_{n_j}(\phi_0)(z)) \geq& W_n^-(z) = \varphi(z+s_1-\varepsilon_1(1-e^{-\sigma n})) - \varepsilon_1\rho(z+s_1)e^{-\sigma n}\\ \geq& \varphi(z+s_1-\varepsilon_1) - \varepsilon_1\rho(z+s_1)e^{-\sigma n}\\ =& \varphi(z+s_1-\frac{s_1-s_0}{2}) - \varepsilon_1\rho(z+s_1)e^{-\sigma n}\\ =& \varphi(z+\frac{s_1+s_0}{2}) - \varepsilon_1\rho(z+s_1)e^{-\sigma n}, \forall z \in \mathbb{R},\ n \in \mathbb{N}^+.\end{aligned}$$

Let $n = n_i - n_j$, and $n_i \to \infty$, we obtain $\phi(\cdot) \geq \varphi(z + \frac{s_1+s_0}{2})$. Denote $s_2 = \frac{s_1+s_0}{2}$, then $s_2 \in (s_0, s_1) \subseteq [s_0, z_0]$, and $\varphi(\cdot + s_2) \leq_{\mathcal{X}} \phi(\cdot)$. By the arbitrariness of $\phi \in \omega(\phi_0)$, we have $\phi(\cdot + s_2) \leq_{\mathcal{X}} \omega(\phi_0)$.

By Theorem 1.1.2, there exists $s_\psi \in [-z_0, z_0]$ such that $\omega(\psi) = h(s_\psi) = \varphi(\cdot + s_\psi)$. Then $\lim_{n\to\infty} \Phi_n(\psi) = \varphi(\cdot + s_\psi)$. Since $U_n(x,\psi) = \bar{U}_n(x - cn, \psi) = \Phi_n(\psi)(x - cn)$, we have $\lim_{n\to\infty} \|U_n(x,\psi) - \varphi(x - cn + s_\psi)\| = 0$ uniformly for $x \in \mathbb{R}$.

Let $\tilde{\varphi}(x-\tilde{c}n)$ be a traveling wave solution (or monotone traveling wave solution) of system (2.3) connecting E^1 to E^2 in case (ii) (or (i)). Clearly, $\tilde{\varphi}$ satisfies (2.14) (or (2.13)) in Lemma 2.3.1. By what we have proved above, there exists $\tilde{s}_\psi \in \mathbb{R}$ such that $\lim_{n\to\infty} \|\tilde{\varphi}(\cdot - \tilde{c}n) - \varphi(\cdot - cn + \tilde{s}_\psi)\| = 0$. By change of variable $\tilde{x} = x - cn$, we have $\lim_{n\to\infty} \|\tilde{\varphi}(\cdot + (c-\tilde{c})n) - \varphi(\cdot + \tilde{s}_\psi)\| = 0$. Since $\tilde{\varphi}(-\infty) = E^1, \tilde{\varphi}(\infty) = E^2$ and $\varphi(\cdot)$ is strictly increasing on $\mathbb{R}$, we then obtain $\tilde{c} = c$, and hence, $\tilde{\varphi}(\cdot) = \varphi(\cdot + \tilde{s}_\psi)$. □

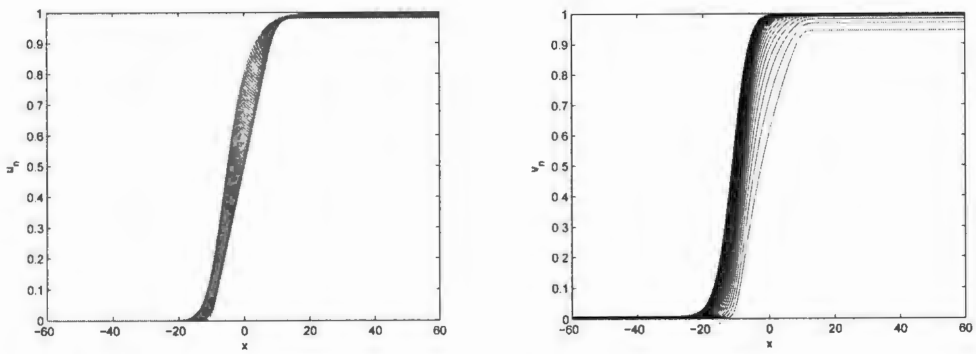
2.4 Numerical simulations

By Theorem 2.3.1, system (2.3) admits a unique monotone bistable traveling wave up to translation, which is globally stable with phase shift. In order to simulate this result, we truncate the infinite domain $\mathbb{R}$ to finite domain $[-L, L]$, where L is sufficiently large. Let $a_1 = 6/5$, $a_2 = 10$, $r_1 = 1/9$, $r_2 = 1/10$, $k_1(y) = \frac{1}{\sqrt{2\pi}} \exp(-y^2/2)$, and $k_2(y) = \frac{1}{\sqrt{4\pi}} \exp(-y^2/4)$. The evolution of the solution is shown in Figure 2.1 for $L = 60$ with the initial condition

$$u_0(x) = \begin{cases} 1/800, & -60 \le x \le -10; \\ 799/800 + 798(x-10)/16000, & -10 \le x \le 10; \\ 799/800, & 10 \le x \le 60. \end{cases}$$

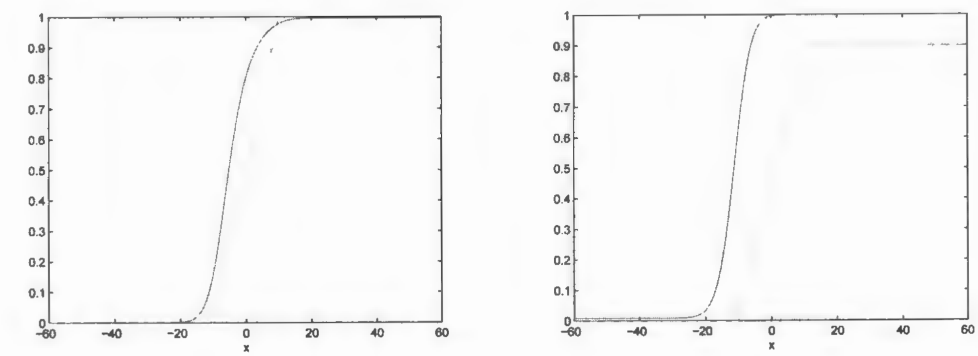
$$v_0(x) = \begin{cases} 1/1000, & -60 \le x \le -10; \\ 899/1000 + 898(x-10)/20000, & -10 \le x \le 10; \\ 899/1000, & 10 \le x \le 60. \end{cases}$$

The numerical wave profile and the initial condition are plotted by solid and dashed lines in Figure 2.2, respectively. We can see, under the given parameters and kernel functions, that the solution rapidly converges to the numerical wave profile, and the sign of the wave speed is negative.



(a) The evolution of u_n. (b) The evolution of v_n.

Figure 2.1: The evolution of u_n and v_n when $n = 1, 2, ..., 20$.



(a) u components. (b) v components.

Figure 2.2: The initial condition and numerical wave profile.

Chapter 3

A Reaction-Diffusion Model with Distributed Delay

3.1 Introduction

In recent years, there have been quite a few research works on biological and dynamical systems with quiescent phases, see [15] and [39] for the tumor growth, [25] for the chemostat, [40] for microbial growth, and [18] for reaction diffusion equations. For more general mathematical properties to such a class of systems, we refer to [16, 17] and references therein. Many researchers have paid attention to reaction-diffusion equations with time delays, see, e.g., [11, 49, 61, 69, 54, 36, 45, 23, 64] and references therein. The authors of [11] investigated the existence of spreading speed and its coincidence with the minimal wave speed for a non-local and time-delayed reaction-diffusion system. In [54] and [36], the authors established the existence, uniqueness and global stability of bistable traveling waves for reaction diffusion equations with finite delays, see also [37] for a time-delayed lattice system with bistable nonlinearity.

Recently, Hadeler and Lutscher [19] proposed the following reaction-diffusion model with distributed delay to describe the evolution of a population in an active phase:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^{+\infty} L(b)u(t-b,x)db - pu + f(u). \tag{3.1}$$

In this model, $u(t,x)$ is the density of the population in the active phase at time t and location x, the dynamics of $u(t,x)$ satisfies the ordinary differential equation $\dot{u} = f(u)$ in a spatially homogenous environment, and $D > 0$ is the diffusion coefficient of the population. We assume that the exit time from the active phase be exponentially distributed with parameter p, and the exit time from the quiescent phase follows an arbitrary distribution with probability density function $L(b) \geq 0$ satisfying $\int_0^\infty L(b)db = 1$. Under appropriate conditions, they obtained the minimal speed of a traveling wave of (3.1) in the case where the function $f(u)$ admits a monostable structure. The purpose of this chapter is to establish the existence of the spreading speed and its coincidence with the minimal wave speed when the function $f(u)$ admits a monostable structure, and the existence and stability of monotone bistable traveling waves when the function $f(u)$ admits a bistable structure. We will appeal to the theory of spreading speeds and traveling waves developed in [13, 28] for monotone semiflows, the finite-delay approximation method introduced in [69], and the squeezing technique used in [54].

This chapter is organized as follows. In section 3.2, we establish the existence of spreading speed and its coincidence with the minimal wave speed in the finite delay case and then generalize the results to infinite delay case. In section 3.3, we obtain the existence of the monotone bistable traveling wave. At last, in section 3.4, we prove the global stability and uniqueness of bistable waves under the assumption that the density function has zero tail.

3.2 Spreading speeds and monostable waves

In this section, we assume that the function f in (3.1) satisfies the following conditions:

$$f(0) = f(1) = 0, \; f'(0) > 0 > f'(1),$$

and

$$f(u) \leq f'(0)u, \; f(u) > 0 \text{ for } u \in (0,1) .$$

Note that (3.1) only admits two constant equilibria $u = 0$ and $u = 1$ in $[0,1]$. We are interested in the existence of the spreading speeds and monostable traveling waves connecting $u = 0$ and $u = 1$.

We first consider the following reaction-diffusion equation with finite delay $\tau > 0$:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^\tau L(b)u(t-b,x)db - pu + f(u). \tag{3.2}$$

Let $\mathcal{C}$ be the space of all bounded and continuous functions from $[-\tau, 0] \times \mathbb{R}$ to $\mathbb{R}$ equipped with the compact open topology, and $\bar{\mathcal{C}} := C([-\tau,0],\mathbb{R}) \subset \mathcal{C}$. Define $F : \mathcal{C} \to C(\mathbb{R},\mathbb{R})$ and $u_t \in \mathcal{C}$ by

$$F(\phi)(x) = p\int_0^\tau L(b)\phi(-b,x)db - p\phi(0,x) + f(\phi(0,x)), \tag{3.3}$$

and

$$u_t(\theta,x) = u(t+\theta,x),$$

for all $(\theta,x) \in [-\tau,0] \times \mathbb{R}$ and $x \in \mathbb{R}$. Then it is easy to verify F is quasi-monotone on $\bar{\mathcal{C}}$ in the sense that $F(\phi) \leq F(\psi)$ whenever $\phi \leq \psi$ in $\bar{\mathcal{C}}$ and $\phi(0) = \psi(0)$.

Note that (3.2) can be written as

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + F(u_t), \forall t > 0, x \in \mathbb{R}. \tag{3.4}$$

From the properties of function f, there exists $\tau_0 > 0$ such that for all $\tau > \tau_0$, the equation

$$F(u) = pu\int_0^\tau L(b)db - pu + f(u) = 0$$

admits only two constant solutions 0 and $u_\tau^* > 0$ in $[0, 1]$ satisfying

$$F'(0) = f'(0) - p(1 - \int_0^\tau L(b)db) > 0,$$

$$F'(u_\tau^*) = f'(u_\tau^*) - p(1 - \int_0^\tau L(b)db) < 0,$$

and $u_\tau^* \to 1$ as $\tau \to \infty$.

Let X be the set of all bounded and continuous functions from $\mathbb{R}$ to $\mathbb{R}$. Clearly, any function in X can be regarded as an element in $\mathcal{C}$. Let $\{T(t)\}_{t\geq 0}$ be the solution semigroup on X determined by the heat equation

$$\frac{\partial u}{\partial t} = D\Delta u,$$

that is

$$T(t)\phi(x) = \int_{\mathbb{R}} \frac{e^{\frac{-y^2}{4Dt}}}{\sqrt{4\pi Dt}}\phi(x-y)dy, \forall \phi \in X,\ t > 0,\ x \in \mathbb{R}.$$

Then equation (3.4) corresponds to the following integral equation:

$$u(t, x) = T(t)u(0, \cdot)(x) + \int_0^t T(t-s)F(u_s)(x)ds,\ \forall t > 0. \tag{3.5}$$

A solution $u(t, x)$ of (3.5) is said to be a mild solution of (3.4), and a function $\bar{u} \in$

$C([-\tau,\infty)\times\mathbb{R},\mathbb{R})$ is called an upper (a lower) solution of (3.5) if it satisfies

$$\bar{u}(t,x) \geq (\leq) T(t)\bar{u}(0,\cdot)(x) + \int_0^t T(t-s)F(\bar{u}_s)(x)ds, \ \forall t>0, \ x\in\mathbb{R}. \tag{3.6}$$

Using a similar argument as used in [11, Lemma 2.1], we have the following Lemma.

Lemma 3.2.1. *For any $\tau > \tau_0$ and $\phi \in \mathcal{C}_{u_\tau^*} := \{\phi \in \mathcal{C} : 0 \leq \phi \leq u_\tau^*\}$, system (3.4) has a unique mild solution $u(t,x;\phi)$ on $[0,\infty)$ and $u(t,x;\phi)$ is a classic solution of (3.4) for $(t,x)\in[\tau,+\infty)\times\mathbb{R}$. For any pair of upper solution $\overline{u}(t,x)$ and lower solutions $\underline{u}(t,x)$ with $\overline{u}(0,x)\geq\underline{u}(0,x)$, then $\overline{u}(t,x)\geq\underline{u}(t,x)$ holds for all $t\geq 0$ and $x\in\mathbb{R}$.*

Let Q_t be the solution map of (3.5), that is,

$$Q_t(\phi)(\theta,x) = u(t+\theta,x;\phi), \ \forall\theta\in[-\tau,0], \ x\in\mathbb{R}, \ \phi\in C_{u_\tau^*},$$

and $\bar{Q}_t$ be the restriction of Q_t to $\bar{\mathcal{C}}_{u_\tau^*}$. Then it is easy to verify that $\bar{Q}_t$ is the solution semiflow on $\bar{\mathcal{C}}_{u_\tau^*}$ associated with the following spatially homogeneous delay differential equation

$$\frac{du}{dt} = \bar{F}(u_t), \ \forall t>0, \tag{3.7}$$

where $\bar{F}$ is the restriction of F to $\bar{\mathcal{C}}_{u_\tau^*}$. Under the assumption that $\int_{\tau-\epsilon}^{\tau} L(b)db > 0$ for all small $\epsilon > 0$, we can verify that (3.7) is cooperative and irreducible. Thus, Theorem 1.1.4 implies that $\bar{Q}_t$ is eventually strongly monotone on $\bar{\mathcal{C}}_{u_\tau^*}$. Note that $\bar{F}$ admits only two constant equilibria 0 and u_τ^* on $\bar{\mathcal{C}}_{u_\tau^*}$, and $\bar{F}'(0) > 0 > \bar{F}'(u_\tau^*)$. It follows from Lemma 1.1.3 that equilibrium 0 is unstable and u_τ^* is globally attractive for (3.7) in $\bar{\mathcal{C}}_{u_\tau^*}\setminus\{0\}$. By the Dancer-Hess connecting orbit Theorem 1.1.1, the semiflow $\bar{Q}_t$ admits a strongly monotone full orbit connecting 0 and u_τ^*. It then follows that Q_t satisfies all assumptions in [28, Theorem 5.1] for all $t\geq 0$. Then we have for each $\tau > \tau_0$, there exists a real number $c_\tau^* > 0$ such that c_τ^* is the spreading speed for solutions of (3.4) with initial functions having compact supports for spatial variable x, and c_τ^* is also the minimal wave speed for monotone traveling waves of (3.4) connecting 0 and u_τ^*.

Theorem 3.2.1. *Let $\tau \geq \tau_0$ be given such that $\int_{\tau-\epsilon}^{\tau} L(b)db > 0$ for all small $\epsilon > 0$, and let $u(t, x, \phi, \tau)$ be the unique solution of (3.4) with the initial data $\phi \in C_{u_\tau^*}$. Then the following statements are valid:*

(1) For any $c > c_\tau^*$, if $\phi \in C_{u_\tau^*}$ with $0 \leq \phi \ll u_\tau^*$ and $\phi(\cdot, x) = 0$ for x outside a bounded interval, then $\lim_{t\to\infty, |x|\geq ct} u(t, x, \phi, \tau) = 0$.

(2) For any $0 < c < c_\tau^*$ and $\sigma \in \bar{C}_{u_\tau^*}$ with $\sigma \gg 0$, there is a positive number r_σ such that if $\phi \in C_{u_\tau^*}$ and $\phi(\cdot, x) \gg \sigma$ for x on an interval of length $2r_\sigma$, then $\lim_{t\to\infty, |x|\leq ct} u(t, x, \phi, \tau) = u_\tau^*$.

(3) For any $c \geq c_\tau^*$, (3.4) has a traveling wave solution $U(x - ct)$ such that $U(s)$ is continuous and nonincreasing in $s \in \mathbb{R}$, and $U(+\infty) = 0$ and $U(-\infty) = u_\tau^*$. Moreover, for any $0 < c < c_\tau^*$, (3.4) has no traveling wave $U(x - ct)$ connecting 0 and u_τ^*.

In order to estimate c_τ^*, we consider the following linear delay differential equation:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^\tau L(b)u(t-b, x)db - pu + f'(0)u. \tag{3.8}$$

Since $f(u) \leq f'(0)u$ for all $0 \leq u \leq 1$ and $f'(0) > 0$, for any $\epsilon \in (0, 1)$, there exists $\delta > 0$ such that

$$f(u) \geq (1-\epsilon)f'(0)u, \forall u \in [0, \delta].$$

It follows that condition (F3) holds in [28, Section 5.1]. Let $\{M_t\}_{t\geq 0}$ be the semiflow associated with (3.8) and $u(t, x) = e^{-\mu x}v(t), \mu > 0$, be a solution of (3.8). It is easy to see that $v(t)$ satisfies the following delay differential equation:

$$\frac{dv}{dt} = D\mu^2 v(t) + p\int_0^\tau L(b)v(t-b)db - pv(t) + f'(0)v(t). \tag{3.9}$$

Define B_μ^t: $\bar{\mathcal{C}} \to \bar{\mathcal{C}}$ by

$$B_\mu^t(v_0)(\theta) = M_t[e^{-\mu x}v_0](\theta, 0),\ \forall\theta \in [-\tau, 0].$$

It then follows that B_μ^t is the solution map of (3.9) with the initial data $v_0 \in \bar{\mathcal{C}}$. Since system (3.9) is cooperative and irreducible (see [52, Section 5.3]), its characteristic equation

$$\lambda - D\mu^2 - f'(0) + p - p\int_0^\tau L(b)e^{-\lambda b}db = 0 \tag{3.10}$$

admits a real principal eigenvalue $\lambda_\tau(\mu)$, which is greater than the real parts of all other roots (see [52, Theorem 5.5.1]). Moreover, by (3.10), it is easy to verify that $\lambda_\tau(\mu) > 0$ provided that $\tau > \tau_0$ large enough. Define function $\Phi_\tau(\mu) = \frac{\lambda_\tau(\mu)}{\mu}$, $\forall\mu > 0$. From the result in [28, Section 5.1], we have

$$c_\tau^* = \inf_{\mu>0} \Phi_\tau(\mu).$$

By the properties of function $\Phi_\tau(\mu)$ as in [28, Lemma 3.8] (see also Lemma 1.2.1), we can verify that there exists a unique $\mu_\tau^* \in (0, +\infty)$ such that $c_\tau^* = \Phi_\tau(\mu_\tau^*)$. From (iii) in Lemma 1.2.1, we see that $\Phi_\tau'(\mu)$ changes the sign at most once in $(0, +\infty)$. Suppose by contradiction that there is a interval $[\mu_1, \mu_2] \subset (0, +\infty)$ such that $c_\tau^* = \Phi_\tau(\mu), \forall\mu \in [\mu_1, \mu_2]$, that is, $c_\tau^*\mu = \lambda_\tau(\mu), \forall\mu \in [\mu_1, \mu_2]$. In view of (3.10), we have

$$c_\tau^*\mu = \lambda_\tau(\mu) = D\mu^2 + f'(0) - p + p\int_0^\tau L(b)e^{-\lambda_\tau(\mu)b}db,$$

and hence

$$f_\tau(\mu) := D\mu^2 + f'(0) - p + p\int_0^\tau L(b)e^{-\lambda_\tau(\mu)b}db - c_\tau^*\mu \equiv 0,\ \forall \mu \in [\mu_1, \mu_2].$$

On the other hand, we have

$$f_\tau'(\mu) = 2D\mu - c_\tau^* - pc_\tau^*\int_0^\tau L(b)e^{-c_\tau^*\mu b}bdb, \forall \mu \in [\mu_1, \mu_2].$$

It is easy to observe that $f_\tau'(\mu)$ is strictly increasing in $[\mu_1, \mu_2]$, which contradicts $f_\tau(\mu) \equiv 0$ for all $\mu \in [\mu_1, \mu_2]$. Therefore, there is a unique $u_\tau^* > 0$ such that (μ_τ^*, c_τ^*) satisfies $c_\tau^* = \Phi_\tau(\mu_\tau^*)$ and $\frac{\partial \Phi_\tau(\mu)}{\partial \mu}|_{\mu_\mu^*} = 0$. Let

$$P_\tau(c, \lambda) = D\mu^2 - c\mu - p + f'(0) + p\int_0^\tau L(b)e^{-\lambda bc}db.$$

Then (μ_τ^*, c_τ^*) can be uniquely determined by

$$P_\tau(c, \mu) = 0 \text{ and } \frac{\partial P_\tau(c, \mu)}{\partial \mu} = 0.$$

By equation (3.10), it is easy to verify that $\lambda_\tau(\mu)$ is nondecreasing with respect to $\tau > \tau_0$ for any $\mu > 0$. Suppose by contradiction that there exist some $\mu_0 > 0$ and $\tau_2 > \tau_1 > 0$ such that $\lambda_{\tau_2}(\mu_0) < \lambda_{\tau_1}(\mu_0)$. Then we see from (3.10) that

$$\begin{aligned}\lambda_{\tau_2}(\mu_0) - \lambda_{\tau_1}(\mu_0) =& p\int_0^{\tau_2} L(b)e^{-\lambda_{\tau_2}(\mu_0)b}db - p\int_0^{\tau_1} L(b)e^{-\lambda_{\tau_1}(\mu_0)b}db \\ \geq& p\int_0^{\tau_1} L(b)(e^{-\lambda_{\tau_2}(\mu_0)b} - e^{-\lambda_{\tau_1}(\mu_0)b})db \geq 0,\end{aligned} \tag{3.11}$$

which is a contradiction. Note that $c_\tau^* = \inf_{\mu>0} \frac{\lambda_\tau(\mu)}{\mu}$ is also a nondecreasing function for all $\tau > \tau_0$. By (3.10), we further have

$$\lambda_\tau(\mu) \leq D\mu^2 + f'(0).$$

Then $\lambda(\mu) := \lim_{\tau\to\infty} \lambda_\tau(\mu) < +\infty$ exists.

Consider the following equation:

$$\lambda = D\mu^2 + f'(0) - p + p\int_0^\infty L(b)e^{-\lambda b}db. \tag{3.12}$$

We claim that $\lambda(\mu)$ is a unique real root of (3.12) for each $\mu > 0$ and the real parts of all other roots of (3.12) are not greater than $\lambda(\mu)$. Suppose there is some $\mu_0 > 0$ and $a \neq \lambda(\mu_0)$ such that a is another root of (3.12). Without loss of generality, we assume that $a > \lambda(\mu_0)(a < \lambda(\mu_0))$. Then we have

$$a - \lambda(\mu_0) = p\int_0^\infty L(b)(e^{-ab} - e^{-\lambda(\mu_0)b})db < 0(> 0),$$

which is a contradiction. Thus, $\lambda(\mu)$ is a unique real root of (3.12). Define function $\Phi(\mu) = \frac{\lambda(\mu)}{\mu}$ for all $\mu > 0$. It is easy to verify that $\Phi(+0) = \Phi(+\infty) = +\infty$. Then $c^* := \inf_{\mu>0}\Phi(\mu)$ must be obtained at some finite μ^*. By the properties of $\Phi_\tau(\mu)$, it follows that (c^*, μ^*) is unique such that $c^* = \Phi(\mu^*)$ and $\frac{d\Phi(\mu)}{d\mu}|_{\mu=\mu^*} = 0$. Let

$$P(c,\mu) = D\mu^2 - c\mu - p + f'(0) + p\int_0^\infty L(b)e^{-\lambda bc}db.$$

Then we can show that the following result holds true.

Lemma 3.2.2. *The following statements are valid*

(1) For any $c > c^*$, there is $\mu > 0$ such that $P(c,\mu) < 0$,

(2) (c^*, μ^*) is uniquely determined by $P(c,\mu) = 0$ and $\frac{\partial P(c,\mu)}{\partial\mu} = 0$,

(3) $\lim_{\tau\to\infty}(c_\tau^*, \mu_\tau^*) = (c^*, \mu^*)$.

Now we consider system (3.1) with infinite time delay. By the argument similar to that in [11, Lemma 2.8.], we have the following result on the existence and uniqueness of solutions of (3.1).

Lemma 3.2.3. *For any* $\phi \in C(-\mathbb{R} \times \mathbb{R}, [0,1])$, (3.1) *has a unique mild solution* $u(t, x; \phi) \in C(\mathbb{R}_- \times \mathbb{R}, [0,1])$ *with initial data* ϕ.

Consider the following linear equation of (3.1):

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^{+\infty} L(b)u(t-b, x)db - pu + f'(0)u. \tag{3.13}$$

In a similar way to (3.6), we define the upper and lower solutions for (3.13). Then we have the following comparison principle. We omit the proof here since it is essentially the same as in [11, Lemma 2.9.].

Lemma 3.2.4. *Assume* $\overline{u}(t,x)$ *and* $\underline{u}(t,x)$ *be the upper and lower solutions of* (3.13). *If* $\overline{u}_0 \geq \underline{u}_0$, *then* $\overline{u}(t,x) \geq \underline{u}(t,x)$, $\forall t \geq 0,\ x \in \mathbb{R}$.

We are now in the position to prove the existence of spreading speed for model (3.1).

Theorem 3.2.2. *Let* $\phi \in C(\mathbb{R}_- \times \mathbb{R}, [0,1])$ *and* $u(t,x;\phi)$ *be the solution of* (3.1) *with* $u_0 = \phi$. *Then the following statements are valid:*

(1) For any $c > c^*$, *if* $\phi(\cdot, x) = 0$ *for* x *outside a bounded interval, then*

$$\lim_{t\to\infty |x|\geq ct} u(t,x;\phi) = 0.$$

(2) For any $0 < c < c^*$ and $\sigma \in \bar{C}_1$ with $\sigma \gg 0$, there is a positive number r_σ such that if $\phi \in C_1$ and $\phi(\cdot, x) \gg \sigma$ for x on an interval of length $2r_\sigma$, then

$$\lim_{t\to\infty, |x|\leq ct} u(t,x;\phi) = 1.$$

Proof. We use the arguments similar to those in [57, Proposition 2.2] and [69, Theorem 2.1]. In the case where $c > c^*$, let $\phi(\theta, x)$ be given as in statement (1). For fixed $\bar{c} \in (c^*, c)$ and $\bar{\lambda} > 0$ such that $P(\bar{c}, \bar{\lambda}) < 0$, there exists a large positive number $M > 0$ such that

$$\phi(t,x) \leq Me^{\bar{\lambda}(\bar{c}t - zx)}, \ \ \forall (t,x) \in (-\infty, 0] \times \mathbb{R}, z = 1 \ or \ z = -1.$$

For $z = 1$ or -1, define $\bar{u}(t,x) = Me^{\bar{\lambda}(\bar{c}t-zx)}$, then $\bar{u}(t,x)$ satisfies

$$\begin{aligned}&\frac{\partial \bar{u}(t,x)}{\partial t} - D\bar{u}_{xx} - p\int_0^{+\infty} L(b)\bar{u}(t-b,x)db + (p - f'(0))\bar{u}(t,x)\\ =&Me^{\bar{\lambda}(\bar{c}t-zx)}(-P(\bar{c},\bar{\lambda})) > 0.\end{aligned} \tag{3.14}$$

That is, $\bar{u}(t,x)$ is an upper solution of (3.13). Since $f(u) \leq f'(0)u$, $u(t,x;\phi)$ is a lower solution of (3.13). Letting $z = \frac{x}{|x|}$, $x \neq 0$. By the comparison principle in Lemma 3.2.4, we obtain

$$u(t,x;\phi) \leq \bar{u}(t,x) = Me^{\bar{\lambda}(\bar{c}t-|x|)} \quad \forall (t,x) \in [0, +\infty) \times \mathbb{R},$$

which implies that

$$\lim_{t\to\infty, |x|\geq ct} u(t,x;\phi) = 0.$$

In the case where $c \in (0, c^*)$, since $\lim_{\tau\to+\infty} c^*_\tau = c^*$, there exists $\tau_1 > \tau_0$ such that

$c_\tau^* > c$ for all $\tau > \tau_1$. For any given $\tau > \tau_1$, we define

$$\hat{\phi}(\theta, x) = \min\{\phi(\theta, x), u_\tau^*\}, \forall(\theta, x) \in [-\tau, 0] \times \mathbb{R}.$$

Let $u(t, x, \tau; \hat{\phi})$ be the solution of (3.2) with $u_0 = \hat{\phi}$. Note that $u(t, x; \phi)$ is an upper solution of (3.2). By the comparison principle in Lemma 3.2.1, we have

$$u(t, x; \phi) \geq u(t, x, \tau; \hat{\phi}), \ \forall(t, x) \in [0, +\infty) \times \mathbb{R},$$

which implies that

$$1 \geq \limsup_{t\to\infty, |x|\leq ct} u(t, x; \phi) \geq \liminf_{t\to\infty, |x|\leq ct} u(t, x; \phi) \geq \liminf_{t\to\infty, |x|\leq ct} u(t, x, \tau; \hat{\phi}) = u_\tau^*, \ \forall\tau > \tau_1.$$

Letting $\tau \to +\infty$, then we have $\lim_{t\to\infty, |x|\leq ct} u(t, x; \phi) = 1$. □

The following results show that the spreading speed $c^* > 0$ obtained above is also the minimum wave speed for monotone traveling waves of system (3.1).

Theorem 3.2.3. *The following statements are valid:*

(1) For any $c \geq c^*$, system (3.1) *has a traveling wave solution $U(x - ct)$ connecting 0 and 1, where $U(\xi)$ is continuous and nonincreasing in $\xi \in \mathbb{R}$.*

(2) For any $0 < c < c^*$, system (3.1)*has no traveling wave solution $U(x - ct)$ connecting 0 and 1.*

Proof. For any given $c > c^*$, we choose a sequence $\tau_n \to \infty$ such that $c_{\tau_n} < c$ and $\lim_{n\to\infty} c_{\tau_n} = c^*$. Then there is a traveling wave $U_n(x + ct)$ such that $U_n(-\infty) = u_n^*$

and $U_n(+\infty) = 0$. Thus, we have

$$\begin{aligned} J_n(U)(\xi) =& DU''(\xi) + cU'(\xi) - pU(\xi) + f(U(\xi)) + p\int_0^{\tau_n} L(b)U(\xi - cb)db \\ =& DU''(\xi) + cU'(\xi) - \alpha U(\xi) + \alpha U(\xi) - pU(\xi) + f(U(\xi)) \\ &+ p\int_0^{\tau_n} L(b)U(\xi - cb)db = 0, \end{aligned} \tag{3.15}$$

where $\alpha > 0$. Define the operator

$$H_n(U)(\xi) = \alpha U(\xi) - pU(\xi) + f(U(\xi)) + p\int_0^{\tau_n} L(b)U(\xi - cb)db. \tag{3.16}$$

Clearly, $\{H_n(U)(\xi)\}_{n=1}^{\infty}$ is uniformly bounded when $U(\xi)$ is bounded. It then follows that

$$\begin{aligned} U(\xi) =& k_1 e^{\lambda_1 \xi} + k_2 e^{\lambda_2 \xi} \\ &+ \frac{1}{D(\lambda_2 - \lambda_1)}\left(\int_{-\infty}^{\xi} e^{\lambda_1(\xi-\eta)} H_n(U)(\eta)d\eta + \int_{\xi}^{+\infty} e^{\lambda_2(\xi-\eta)} H_n(U)(\eta)d\eta\right), \end{aligned} \tag{3.17}$$

where k_1, k_2 are arbitrary constants and

$$\lambda_1 = \frac{-c - \sqrt{c^2 + 4D\alpha}}{2D} < 0, \quad \lambda_2 = \frac{-c + \sqrt{c^2 + 4D\alpha}}{2D} > 0. \tag{3.18}$$

Since $U_n(\xi)$ satisfies (3.15) and is bounded, it follows that $U_n(\xi)$ satisfies (3.17) with $k_1 = k_2 = 0$, that is,

$$U_n(\xi) = \frac{1}{D(\lambda_2 - \lambda_1)}\left(\int_{-\infty}^{\xi} e^{\lambda_1(\xi-\eta)} H_n(U_n)(\eta)d\eta + \int_{\xi}^{+\infty} e^{\lambda_2(\xi-\eta)} H_n(U_n)(\eta)d\eta\right).$$

Thus, $U_n'(\xi), U_n''(\xi), U_n'''(\xi)$ are uniformly bounded for $n \geq \tau$ from the uniform boundedness of $U_n(\xi)$ and $H_n(U_n)(\xi)$. By the spatial translation invariance of the original equation, we can assume $U_n(0) = \frac{1}{2}$. By the Arizela-Ascoli theorem and a diagonal procedure, it follows that $\{U_n(\xi), U_n'(\xi), U_n''(\xi)\}$ has a convergent subsequence, which is convergent uniformly on each compact set in $\mathbb{R}$. Without loss of generality, denote $U_n(\xi) \to U^*(\xi)$. Then we have

$$(U_n(\xi), U_n'(\xi), U_n''(\xi)) \to (U^*(\xi), U^{*\prime}(\xi), U^{*\prime\prime}(\xi)).$$

Define

$$J(U)(\xi) = DU''(\xi) + CU'(\xi) - pU(\xi) + f(U(\xi)) + p\int_0^{+\infty} L(b)U(\xi - cb)db.$$

Then $\lim_{n\to\infty} J_n(U_n)(\xi) = J(U^*)(\xi)$ pointwise, which implies that $U^*(\xi)$ is a solution of $J(U)(\xi) = 0$. Since $U_n(\xi)$ is nonincreasing and $U_n(-\infty) = u_n^*, U_n(\infty) = 0$, $U^*(\xi)$ is nonincreasing and bounded. Therefore $U^*(+\infty)$ exists and satisfies the following equation

$$-px + f(x) + p\int_0^{\infty} L(b)db = f(x) = 0. \tag{3.19}$$

Then we have

$$U^*(-\infty) = 1 > \frac{1}{2} = U^*(0) > U^*(+\infty) = 0.$$

Therefore, $U^*(\xi)$ is a traveling wave solution of (3.1).

For $c = c^*$, by the same limiting argument as those in [69, Theorem 3.1], we can obtain the existence of monotone traveling wave $U(x - c^*t)$ connecting 1 to 0. The nonexistence of traveling wave can be proven by the contradiction argument as used in [69, Theorem 3.1]. $\square$

3.3 Existence of bistable waves

In this section, we consider the case where function f has three zero points $0 < x^* < 1$ on $[0, 1]$ satisfying

$$f'(0) < 0, \;\; f'(x^*) > 0 \;\; \text{and} \;\; f'(1) < 0.$$

We establish the existence of the wavefronts connecting two stable equilibria 0 and 1.

Let $\tau \geq \tau_0$ large enough such that the delay equation

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^\tau L(b)u(t-b,x)db - pu + f(u) \tag{3.20}$$

admits only three constant equilibria $0 < \alpha_\tau < \beta_\tau$ on $[0, 1]$ satisfying $\lim_{\tau\to\infty}\alpha_\tau = x^*$ and $\lim_{\tau\to\infty}\beta_\tau = 1$, and F, as defined in (3.3), satisfies $F'(0) < 0$, $F'(\alpha_\tau) > 0$, and $F'(\beta_\tau) < 0$. We first establish the existence of the nondecreasing bistable traveling waves for (3.20) connecting 0 and β_τ.

Define function $\bar{F}$ on $\mathcal{C}$ by $\bar{F}(\phi) = p\int_0^\tau L(b)\phi(-b)db - p\phi(0) + f(\phi(0))$. Then we have

$$\begin{aligned} D\bar{F}(\phi)h =& (f'(\phi(0)) - p)h(0) + p\int_0^\tau h(-b)L(b)db \\ =& (f'(\phi(0)) - p)h(0) + p\int_{-\tau}^0 h(b)L(-b)db \\ =& (f'(\phi(0)) - p)h(0) + p\int_{-\tau}^0 h(b)d\eta(\phi), \end{aligned} \tag{3.21}$$

where $\eta(\phi)$ is a positive Borel measure on $[-\tau, 0]$ defined as $\eta(\phi)\Omega = \int_\Omega L(-b)db$ for any measurable subset $\Omega \subset [-\tau, 0]$. Since $L(b) \geq 0$ and $\int_0^\infty L(b)db > 0$, without loss of generality, we assume that τ is chosen such that $\eta(\phi)[-\tau, -\tau+\epsilon] = \int_{-\tau}^{-\tau+\epsilon} L(-b)db > 0$ for all small $\epsilon > 0$. Thus, assumption (D4) holds in Theorem 1.2.8.

For any $\epsilon > 0$, define a linear operator $L_\epsilon : \mathcal{C}_{\beta_\tau} \to C(\mathbb{R}, \mathbb{R})$ by

$$L_\epsilon \phi = p \int_0^\tau L(b)\phi(-b, x)db - p\phi(0, x) + (1 - \epsilon)f'(\alpha_\tau)\phi(0, x).$$

Then $L_\epsilon \phi \to DF(\alpha_\tau)\phi$ as $\epsilon \to 0$, where the operator $DF(\alpha_\tau)$ defined by

$$DF(\alpha_\tau)\phi = p \int_0^\tau L(b)\phi(-b, x)db - p\phi(0, x) + f'(\alpha_\tau)\phi(0, x).$$

It is easy to verify that there exists $\delta \in (0, \beta_\tau)$ such that

$$F(\alpha_\tau + \phi) \geq L_\epsilon(\phi) \text{ and } F(\alpha_\tau - \phi) \leq -L_\epsilon(\phi), \forall \phi \in \mathcal{C}_\delta,$$

that is, assumption (D5) holds. Further, assumptions (D1)-(D3) are also satisfied. Thus, by Theorem 1.2.8, we have the following result.

Theorem 3.3.1. *Let $\tau \geq \tau_0$ be given such that $\int_{\tau-\epsilon}^{\tau} L(b)db > 0$ for all small $\epsilon > 0$. Then system* (3.20) *admits a nondecreasing traveling wave $V_\tau(x - c_\tau t)$ with $V_\tau(-\infty) = 0$ and $V_\tau(+\infty) = \beta_\tau$.*

To prove the boundedness of $\{c_\tau\}_{\tau \geq \tau_0}$, we use the similar ideas to those in [12] to construct upper and lower solutions. Choose increasing function $\rho \in C^2(R, R)$ such that

$$\rho(\xi) = 0,\ \forall \xi \leq 0;\quad \rho'(\xi) \in (0, 1),\ \forall \xi \in (0, 4);$$

$$\rho(\xi) = 1,\ \forall \xi \geq 4;\quad |\rho''(\xi)| \leq 1,\ \forall \xi \in (0, 4).$$

Then we have the following result.

Lemma 3.3.1. *Define*

$$\underline{v}(t, x) = v_-(x - ct; \delta, \sigma) := \rho(\sigma(x - ct)) - \delta,$$

$$\overline{v}(t,x) = v_+(x+ct;\delta,\sigma) := \rho(\sigma(x+ct)) + \delta.$$

Then there exist $\bar{\delta} > 0$, $\bar{\sigma} > 0$ and $\bar{c} > 0$ such that for any $\delta \in [\bar{\delta}/2, \bar{\delta}]$, $\sigma \in [\bar{\sigma}/2, \bar{\sigma}]$ and $c \geq \bar{c}$, $\underline{v}(t,x)$ and $\overline{v}(t,x)$ are a lower solution and an upper solution of (3.20) *with $\tau > \tau_0$, respectively.*

Proof. Define $F_\infty : \mathbb{R} \to \mathbb{R}$ by

$$F_\infty(x) = px \int_0^\infty L(b)db - px + f(x).$$

Then $F'_\infty(0) = f'(0) < 0$, $F'_\infty(x^*) = f'(x^*) > 0$ and $F'_\infty(1) = f'(1) < 0$. By the continuous differentiability of F_∞, there exists $0 < \bar{\delta} < 1$ such that for all $\delta \in [0, \bar{\delta}]$ the following inequalities hold:

$$F_\infty(-\delta) \geq -F'_\infty(0)\delta + \frac{1}{2}f'(0)\delta = -\frac{1}{2}f'(0)\delta > 0,$$

$$F_\infty(1-\delta) \geq -F'_\infty(1)\delta + \frac{1}{2}f'(1)\delta = -\frac{1}{2}f'(0)\delta > 0.$$

Thus, we can find $\theta_0 > 0$, $\bar{\sigma} > 0$ such that for any $\theta \in [0, \theta_0]$, $\sigma \in [0, \bar{\sigma}]$ and $\delta \in [\frac{\bar{\delta}}{2}, \bar{\delta}]$, the following two inequalities hold:

$$F_\infty(\theta - \delta) > D\sigma^2 + p\int_{\tau_0}^\infty L(b)db,$$

$$F_\infty((1-\theta) - \delta) > D\sigma^2 + p\int_{\tau_0}^\infty L(b)db,$$

where we may ask τ_0 large enough if it is necessary.

Letting $\xi = x - ct$, we then have

$$\begin{aligned}
&D\frac{\partial^2 \underline{v}}{\partial x^2} - \frac{\partial \underline{v}}{\partial t} + F(\underline{v}_t)(x)\\
=&Dv_-''(x-ct) + cv_-'(x-ct) + F(\underline{v}_t)(x)\\
=&Dv_-''(\xi) + cv_-'(\xi) - pv_-(\xi) + f(v_-(\xi)) + p\int_0^\tau L(b)(\rho(\sigma(\xi+cb)) - \delta)db\\
\geq&D\sigma^2\rho''(\sigma\xi) + c\sigma\rho'(\sigma\xi) - pv_-(\xi) + f(v_-(\xi)) + p\int_0^\tau L(b)(\rho(\sigma(\xi)) - \delta)db\\
=&D\sigma^2\rho''(\sigma\xi) + c\sigma\rho'(\sigma\xi) + F_\infty(v_-(\xi)) - pv_-(\xi)\int_\tau^\infty L(b)db\\
\geq&D\sigma^2\rho''(\sigma\xi) + c\sigma\rho'(\sigma\xi) + F_\infty(v_-(\xi)) - p\int_{\tau_0}^\infty L(b)db
\end{aligned} \tag{3.22}$$

Denote $m := \min_{\rho(\xi)\in[\theta_0,1-\theta_0]}\rho'(\xi) > 0$ and $F_{\min} := \min_{-1\leq x\leq 1} F_\infty(x)$. Let $\bar{c} > 0$ sufficiently large such that

$$c\sigma m \geq -F_{\min} + D\sigma^2 + p\int_{\tau_0}^\infty L(b)db,\ \forall c > \bar{c}.$$

If $\rho(\sigma\xi) \in [0,\theta_0] \cup [1-\theta_0, 1]$, then

$$D\frac{\partial^2 \underline{v}}{\partial x^2} - \frac{\partial \underline{v}}{\partial t} + F(\underline{v}_t)(x) \geq -D\sigma^2 + D\sigma^2 + p\int_{\tau_0}^\infty L(b)db - p\int_{\tau_0}^\infty L(b)db = 0;$$

If $\rho(\sigma\xi) \in [\theta_0, 1-\theta_0]$, then

$$D\frac{\partial^2 \underline{v}}{\partial x^2} - \frac{\partial \underline{v}}{\partial t} + F(\underline{v}_t)(x) \geq -D\sigma^2 + c\sigma m + F_{\min} - p\int_{\tau_0}^\infty L(b)db \geq 0.$$

Consequently, $\underline{v}(t,x)$ is a lower solution of (3.20). Similarly, we can prove $\overline{v}(t,x)$ is an upper solution of (3.20). □

Lemma 3.3.2. *$\{c_\tau\}_{\tau\geq\tau_0}$ is bounded.*

Proof. By Lemma 3.3.1, we see that there exist $\bar{c}$, $\bar{\delta}$ and $\bar{\sigma}$ independent of $\tau \geq \tau_0$ such that $v_-(x-\bar{c}t;\bar{\delta},\bar{\sigma})$ and $v_+(x+\bar{c}t;\bar{\delta},\bar{\sigma})$ are a lower and an upper solution of system (3.20), respectively. Note that when τ_0 large enough, the following inequalities hold:

$$v_-(-\infty;\bar{\delta},\bar{\sigma}) = -\bar{\delta} < 0 = V_\tau(-\infty),$$

$$v_-(+\infty;\bar{\delta},\bar{\sigma}) = 1-\bar{\delta} < \beta_\tau = V_\tau(+\infty).$$

Since v_- and V_τ are all nondecreasing functions, there exists $\xi_\tau \in \mathbb{R}$ such that

$$V_\tau(\xi+\xi_\tau) \geq v_-(\xi;\bar{\delta},\bar{\sigma}),\ \forall \xi \in \mathbb{R}.$$

By the comparison principle, we then have

$$V_\tau(x-c_\tau t+\xi_\tau) \geq v_-(x-\bar{c}t;\bar{\delta},\bar{\sigma}),\ \forall t \geq 0,\ x \in \mathbb{R}.$$

Thus, we obtain

$$V_\tau(\cdot+(\bar{c}-c_\tau)t+\xi_\tau) \geq v_-(\cdot;\bar{\delta},\bar{\sigma}),\ \forall t \geq 0,$$

which implies that $c_\tau \leq \bar{c}$, $\forall \tau \geq \tau_0$. Suppose, by contradiction, that $c_\tau > \bar{c}$. Then we have $0 = V_\tau(-\infty) \gg 0$, which is a contradiction. Similarly, we can prove $c_\tau \geq -\bar{c}$. Therefore, we have $|c_\tau| \leq \bar{c}$ for all $\tau > \tau_0$. $\square$

Lemma 3.3.3. *The following statements are valid:*

(1) If $U(x+ct)$ is a nondecreasing traveling wave of (3.1) *with $U(-\infty) = x^*$ and $U(+\infty) = 1$, then $c > 0$.*

(2) If $U(x+ct)$ is a nondecreasing traveling wave of (3.1) *with $U(-\infty) = 0$ and $U(+\infty) = x^*$, then $c < 0$.*

Proof. Let $U(x+ct)$ be a nondecreasing traveling waves in (1), by the spatial symmetry of (3.1). Then $W(x-ct) := U(-x+ct) = U(-(x-ct))$ is a nonincreasing traveling wave of (3.1) with $W(-\infty) = 1$ and $W(+\infty) = x^*$. By a similar analysis as we did in Section 2, we have the similar results as Theorem 3.2.3 for system (3.1) restricted on $[x^*, 1]$, that is, there is a positive number c_1 such that $c > c_1 > 0$.

If $U(x+ct)$ is a nondecreasing traveling waves in (2), then $\bar{W}(x+ct) = x^* - U(x+ct)$ is a nonincreasing traveling wave of the following system:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^{+\infty} L(b)u(t-b,x)db - pu - f(x^* - u), \tag{3.23}$$

with $\bar{W}(-\infty) = x^*$ and $\bar{W}(+\infty) = 0$. Similarly, for system (3.23) restricted on $[0, x^*]$, there is a positive number $c_0 > 0$ such that $-c > c_0 > 0$, which implies that $c < 0$. □

Now we are in a position to show the main result of this section.

Theorem 3.3.2. *System* (3.1) *admits a nondecreasing bistable traveling wave* $U(x - ct)$ *with* $U(-\infty) = 0$ *and* $U(+\infty) = 1$.

Proof. From Lemma 3.3.2, we see that $\{c_\tau\}_{\tau > \tau_0}$ is bounded. Then there is a sequence $n_k > \tau_0$, $k \in \mathbb{N}$ such that c_{n_k} converges to some real number c as $n_k \to +\infty$. Let (U_{n_k}, c_{n_k}) be the corresponding wavefront of (3.20) with $\tau = n_k$. Then $\{U_{n_k}\}_{k\geq 1}$ is a sequence of monotone functions with $U_{n_k}(-\infty) = 0$ and $U_{n_k}(+\infty) = 1$. Thus, there exist $\xi_k, \eta_k \in \mathbb{R}$ such that $U_{n_k}(\xi_k) = \frac{x^*}{2}$ and $U_{n_k}(\eta_k) = \frac{1+x^*}{2}$. Let

$$V_k(\cdot) = U_{n_k}(\cdot + \xi_k) \text{ and } W_k(\cdot) = U_{n_k}(\cdot + \eta_k).$$

Then $V_k(0) = \frac{x^*}{2}$ and $W_k(0) = \frac{1+x^*}{2}$ for all $k \geq 1$. Note that $\{V_k\}_{k\geq 1}$ and $\{W_k\}_{k\geq 1}$ are monotone function sequences with $V_k(-\infty) = W_k(-\infty) = 0$ and $V_k(+\infty) = W_k(+\infty) = 1$. By Helly's theorem, it follows that there exist subsequences, still denote as $\{V_k\}_{k\geq 1}$ and $\{W_k\}_{k\geq 1}$, and monotone functions V and W such that $\lim_{k\to\infty} V_k = V$

and $\lim_{k\to} W_k = W$ pointwise on $\mathbb{R}$ as $k \to +\infty$ with $V(0) = \frac{x^*}{2}$ and $W(0) = \frac{1+x^*}{2}$. Denote $V_\pm(\cdot) = V(\cdot \pm 0)$ and $W_\pm(\cdot) = W(\cdot \pm)$. Then V_- and W_- are left-continuous, while V_+ and W_+ are right-continuous. Note that $V_\pm(\xi) = V(\xi)$ and $W_\pm(\xi) = W(\xi)$ almost everywhere on $\mathbb{R}$.

Now we claim that both (V, c) and (W, c) are traveling wavefronts of (3.1). Note that V_k satisfies the following system:

$$DV_k''(\xi) + c_{n_k} V_k'(\xi) - pV_k(\xi) + p\int_0^{n_k} L(b)V_k(\xi + cb)db + f(V_k(\xi)) = 0, \tag{3.24}$$

which is equivalent to the following integral equation

$$\begin{aligned} V_k(\xi) = & \frac{1}{\sqrt{c_{n_k}^2 + 4Dp}}\{\int_{-\infty}^{\xi} e^{\lambda_{1k}(\xi-\eta)}(p\int_0^{n_k} L(b)V_k(\eta + cb)db + f(V_k(\eta))d\eta \\ & + \int_{\xi}^{+\infty} e^{\lambda_{2k}(\xi-\eta)}(p\int_0^{n_k} L(b)V_k(\eta + cb)db + f(V_k(\eta))d\eta\}, \end{aligned} \tag{3.25}$$

where $\lambda_{1k} = \frac{-c_{n_k} - \sqrt{c_{n_k}^2 + 4Dp}}{2D} < 0$ and $\lambda_{2k} = \frac{-c_{n_k} + \sqrt{c_{n_k}^2 + 4Dp}}{2D} > 0$. Further,

$$\lambda_1 = \lim_{n\to\infty} \lambda_{1k} = \frac{-c - \sqrt{c^2 + 4Dp}}{2D},$$

$$\lambda_2 = \lim_{n\to\infty} \lambda_{2k} = \frac{-c + \sqrt{c^2 + 4Dp}}{2D}.$$

By the Lebesgue dominated convergence theorem, it then follows that

$$\begin{aligned} V(\xi) = & \frac{1}{\sqrt{c^2 + 4Dp}}\{\int_{-\infty}^{\xi} e^{\lambda_1(\xi-\eta)}(p\int_0^{+\infty} L(b)V(\eta + cb)db + f(V(\eta))d\eta \\ & + \int_{\xi}^{+\infty} e^{\lambda_2(\xi-\eta)}(p\int_0^{+\infty} L(b)V(\eta + cb)db + f(V(\eta))d\eta\}, \end{aligned} \tag{3.26}$$

which is equivalent to

$$DV''(\xi) + cV'(\xi) - pV(\xi) + p\int_0^{\infty} L(b)V(\xi + cb)db + f(V(\xi)) = 0, \tag{3.27}$$

that is, $V(x - ct)$ satisfies equation (3.1). Similarly, we can prove $W(x - ct)$ also satisfies equation (3.1).

Now we need to prove the boundary conditions. It is obvious that $V(\pm\infty)$ and $W(\pm\infty)$ exist from the monotonicity of V and W. Note that $V(\pm\infty)$ and $W(\pm\infty)$ are the zero points of $f(u) = 0$. Since $V(0) = \frac{x^*}{2}$ and $W(0) = \frac{1+x^*}{2}$, it follows that $V(-\infty) = 0$ and $V(+\infty) = x^*$ or 1, and $W(-\infty) = x^*$ or 0, and $W(+\infty) = 1$. Note that W and V are all traveling wave solution of 3.1. By Lemma 3.3.3, we see that $V(+\infty) = x^*$ and $W(-\infty) = x^*$ cannot happen simultaneously. Thus, (V, c) or (W, c) is a wavefront of (3.1) connecting 0 and 1. □

3.4 Global stability of bistable waves

In this section, we prove the global asymptotic stability with shift and uniqueness of monotone bistable traveling waves. Note that it is much more difficult to analyze the global stability of traveling waves for an infinite delay model. So we assume that there exists $\tau > 0$ such that $L(b) \equiv 0$ for all $b \geq \tau$. Accordingly, system (3.1) becomes the following differential equation with finite distributed delay:

$$\frac{\partial u}{\partial t} = D\frac{\partial^2 u}{\partial x^2} + p\int_0^{\tau} L(b)u(t - b, x)db - pu + f(u). \tag{3.28}$$

Let $u(t, x) = U(x - ct)$ be the monotone bistable traveling wave solution of (3.28) obtained in the Section 3.3. Then we have $U'(\xi) \geq 0$ and $U'(\xi) \not\equiv 0$ for all $\xi \in \mathbb{R}$. Let

$v(t,x) = \frac{\partial u(t,x)}{x}$. Then $v(t,x)$ satisfies the following equation:

$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial x^2} + p\int_0^\tau L(b)v(t-b,x)db - pv + f'(u)v. \tag{3.29}$$

By the strong maximum principle, it follows that $v(t,x) > 0$ for all $t > 0$, and hence, $U'(\xi) > 0$ for all $\xi \in \mathbb{R}$.

Lemma 3.4.1. *Let $U(x-ct)$ be a strictly monotone bistable traveling wave solution of* (3.28). *Then there exist positive numbers β_0, σ_0, and $\bar{\delta}$ such that for any $\delta \in (0,\bar{\delta}]$ and every $\zeta_0 \in \mathbb{R}$, the functions $w^{\pm}$ defined by*

$$w^{\pm}(t,x) := U(x - ct + \zeta_0 \pm \sigma_0\delta[1 - e^{-\beta_0 t}]) \pm \delta e^{-\beta_0 t}$$

are an upper solution and a lower solutions of (3.28) *on* $[0,+\infty)$, *respectively.*

Proof. Without loss of generality, we assume $\zeta_0 = 0$. Note that $f(0) = f(1) = 0$, $f'(0) < 0$, and $f'(1) < 0$. Then there exist $L_1 > 0$ and $\delta^* \in (0,1)$ such that

$$f(x) > 0, x \in [-\delta^*, 0) \text{ and } f'(x) < -L_1, x \in [-\delta^*, \delta^*];$$

$$f(x) > 0, x \in (1, \delta^*] \text{ and } f'(x) < -L_1, x \in [1-\delta^*, 1+\delta^*].$$

Since $U(-\infty) = 0$ and $U(+\infty) = 1$, there exists $M > 0$ such that

$$U(\xi) \in [-\frac{\delta^*}{2}, \frac{\delta^*}{2}], \xi < -M \text{ and } U(\xi) \in [1-\frac{\delta^*}{2}, 1+\frac{\delta^*}{2}], \xi > M.$$

Let $\bar{\delta} = \frac{\delta^*}{2}$, $L_2 = \min_{\xi \in [-M,M]} U'(\xi) > 0$ and $L_3 = \max_{x \in [0,1+\bar{\delta}]} f(x) > 0$. Fix $\beta_0 > 0$ small such that $\beta_0 + p\left(\int_0^\tau L(b)e^{\beta_0 b}db - 1\right) < L_1$ and $\sigma_0 = \frac{2(L_1+L_3)}{L_2\beta_0} > 0$. It is easy to verify that function $U(\xi)$ satisfies

$$DU''(\xi) + cU'(\xi) + p\int_0^\tau L(b)U(\xi + cb)db - pU(\xi) + f(U(\xi)) = 0, \ \forall \xi \in \mathbb{R}.$$

Denote $\xi(t) := x - ct + \sigma_0\delta(1 - e^{-\beta_0 t})$. Then for any $t \geq 0$ and $\delta \in (0, \bar{\delta})$, we have

$$\begin{aligned}
&\frac{\partial w^+(x,t)}{\partial t} - D\frac{\partial^2 w^+(x,t)}{\partial x^2} - F(w^+(t,x)) \\
=&U'(\xi)[-c + \sigma_0\delta\beta_0 e^{-\beta_0 t}] - \delta\beta_0 e^{-\beta_0 t} - DU''(\xi) + pU(\xi) + p\delta e^{-\beta_0 t} \\
&- p\int_0^\tau L(b)[U(x - ct + cb + \sigma_0\delta(1 - e^{-\beta_0(t-b)})) + \delta e^{-\beta_0(t-b)}]db - f(U(\xi) + \delta e^{-\beta_0 t}) \\
=&p\int_0^\tau L(b)[U(\xi + cb) - U(\xi + cb + \sigma_0\delta e^{-\beta_0 t}(1 - e^{\beta_0 b}))]db - p\delta e^{-\beta_0 t}\int_0^\tau L(b)e^{\beta_0 b}db \\
&+ \sigma_0\delta\beta_0 e^{-\beta_0 t}U'(\xi) - \delta\beta_0 e^{-\beta_0 t} + p\delta e^{-\beta_0 t} + f(U(\xi)) - f(U(\xi) + \delta e^{-\beta_0 t}) \\
\geq&\delta e^{-\beta_0 t}[-p\int_0^\tau L(b)e^{\beta_0 b}db + \sigma_0\beta_0 U'(\xi) - \beta_0 + p - f'(U(\xi) + \theta\delta e^{-\beta_0 t})] \\
=&\delta e^{-\beta_0 t}[\sigma_0\beta_0 U'(\xi) - \beta_0 - p(\int_0^\tau L(b)e^{\beta_0 b}db - 1) - f'(U(\xi) + \theta\delta e^{-\beta_0 t})], \ \theta \in (0,1)
\end{aligned}$$

In the case where $|\xi(t)| > M$, by the choice of $\bar{\delta}$, β_0 and $\theta \in (0,1)$, we have

$$U(\xi) + \theta\delta e^{-\beta_0 t} \in [0, \delta^*] \text{ or } U(\xi) + \theta\delta e^{-\beta_0 t} \in [1, 1 + \delta^*],$$

which implies that $f'(U(\xi) + \theta\delta e^{-\beta_0 t})) < -L_1$. It then follows that

$$\frac{\partial w^+(x,t)}{\partial t} - D\frac{\partial^2 w^+(x,t)}{\partial x^2} - F(w^+(t,x)) \geq \delta e^{-\beta_0 t}[-\beta_0 - p(\int_0^\tau L(b)e^{\beta_0 b}db - 1) + L_1] \geq 0;$$

In the case where $|\xi(t)| \leq M$, we have

$$\frac{\partial w^+(x,t)}{\partial t} - D\frac{\partial^2 w^+(x,t)}{\partial x^2} - F(w^+(t,x)) \geq \delta e^{-\beta_0 t}[\sigma_0\beta_0 L_2 - L_1 - L_3] = L_1 + L_3 > 0.$$

Similarly, we can verify w^- is a lower solution of system (3.28). $\square$

Let $\tilde{\delta} = \min\{\frac{x^*}{2}, \frac{1-x^*}{2}, \delta^*\}$, and $\rho(\cdot) \in C^2(\mathbb{R}, \mathbb{R})$ be the function defined in Section 3. Then we have the following result.

Lemma 3.4.2. *For any $\delta \in (0, \tilde{\delta}]$, there exist two positive number ϵ and C such that for any $\xi \in R$, the functions v^+ and v^- defined by*

$$\begin{aligned} v^+(t,x) =& (1+\delta) - [1 - (x^* - 2\delta)e^{-\epsilon t}]\rho(-\epsilon(x - \xi + Ct)), \\ v^-(t,x) =& -\delta + [1 - (1 - x^* - 2\delta)e^{-\epsilon t}]\rho(\epsilon(x - \xi - Ct)), \end{aligned} \tag{3.30}$$

are an upper solution and a lower solutions of system (3.28) *on* $[0, \infty)$*, respectively.*

Proof. Without loss of generality, we take $\xi = 0$. We first verify that v^- is a lower solution. For any $\delta \in (0, \tilde{\delta}]$, we choose $\varepsilon = \varepsilon(\delta) > 0$ small enough such that the following three inequalities hold:

$$(1 - x^*)e^{\varepsilon\tau} < 1,$$

$$-D\varepsilon^2 - \varepsilon - p\tau\varepsilon + \min_{u \in [-\delta, -\frac{\delta}{2}]} f(u) > 0,$$

and

$$-D\varepsilon^2 - \varepsilon - p\tau\varepsilon + \min_{u \in [x^* + \frac{\delta}{2}, 1-\delta]} f(u) > 0.$$

It is easy to verify that $v^-(x,t) \in [-\delta, 1-\delta]$ for all $x \in R$ and $t \geq -\tau$. Choose $C = C(\delta) > 0$ large enough such that

$$-D\varepsilon^2 - \varepsilon + \varepsilon C[1 - (1 - x^*)e^{\varepsilon\tau}] \cdot \min_{\rho(s) \in [\frac{\delta}{2}, 1-\frac{\delta}{2}]} \rho'(s) - p\tau\varepsilon + \min_{u \in [-\delta, 1-\delta]} f(u) > 0.$$

Denote $\zeta = \varepsilon(x - Ct)$. Then for any $t \geq -\tau$, the following inequalities hold:

$$
\begin{aligned}
\frac{\partial v^-(t,x)}{\partial t} =& - C\varepsilon[1 - (1 - x^* - 2\delta)e^{-\varepsilon t}]\rho'(\zeta) + \varepsilon(1 - x^* - 2\delta)e^{-\varepsilon t}\rho(\zeta) \\
\leq& - C\varepsilon[1 - (1 - x^* - 2\delta)e^{-\varepsilon\tau}]\rho'(\zeta) + \varepsilon(1 - x^* - 2\delta)e^{-\varepsilon\tau}\rho(\zeta) \\
\leq& - C\varepsilon[1 - (1 - x^*)e^{-\varepsilon\tau}]\rho'(\zeta) + \varepsilon(1 - x^*)e^{-\varepsilon\tau}\rho(\zeta) \\
\leq& \varepsilon.
\end{aligned}
$$

It then follows that

$$
\begin{aligned}
& D\frac{\partial v^-(t,x)}{\partial x^2} - \frac{\partial v^-(t,x)}{\partial t} + F(v^-(t,x)) \\
=& D[1 - (1 - x^* - 2\delta)e^{-\varepsilon t}]\varepsilon^2\rho''(\zeta) + C\varepsilon[1 - (1 - x^* - 2\delta)e^{-\varepsilon t}]\rho'(\zeta) \\
& - \varepsilon(1 - x^* - 2\delta)e^{-\varepsilon t}\rho(\zeta) + p\int_0^\tau L(b)v^-(x, t-b)db - pv^-(x,t) + f(v^-(x,t)) \\
\geq& - D\varepsilon^2 + C\varepsilon[1 - (1 - x^*)e^{\varepsilon\tau}]\rho'(\zeta) - \varepsilon + p\int_0^\tau L(b)v^-(x, t-b)db \\
& - pv^-(x,t) + f(v^-(x,t)), \quad \forall t \geq 0.
\end{aligned}
\tag{3.31}
$$

Then we discuss (3.31) in the following three cases.

Case (i) If $\rho(\zeta) < \frac{\delta}{2}$, it is easy to verify that $v^-(x,t) \in [-\delta, -\frac{\delta}{2}]$ for all $x \in \mathbb{R}$ and

$t \geq -\tau$. Then we have

$$
\begin{aligned}
&D\frac{\partial v^-(t,x)}{\partial x^2} - \frac{\partial v^-(t,x)}{\partial t} + F(v^-(t,x)\\
\geq &- D\varepsilon^2 - \varepsilon + p\int_0^\tau L(b)v^-(x,t-b)db - pv^-(x,t) + f(v^-(x,t))\\
\geq &- D\varepsilon^2 - \varepsilon + p\min_{s\in[t-\tau,t]} v^-(x,s) - pv^-(x,t) + \min_{u\in[-\delta,-\frac{\delta}{2}]} f(u)\\
= &- D\varepsilon^2 - \varepsilon + p(v^-(x,t^*) - v^-(x,t)) + \min_{u\in[-\delta,-\frac{\delta}{2}]} f(u), \quad t^* \in [t-\tau,t]\\
\geq &- D\varepsilon^2 - \varepsilon + p(t^*-t)\max_{s\in[t^*,t]} \frac{\partial v^-(x,s)}{\partial s} + \min_{u\in[-\delta,-\frac{\delta}{2}]} f(u)\\
\geq &- D\varepsilon^2 - \varepsilon + p(t^*-t)\varepsilon + \min_{u\in[-\delta,-\frac{\delta}{2}]} f(u)\\
\geq &- D\varepsilon^2 - \varepsilon - p\tau\varepsilon + \min_{u\in[-\delta,-\frac{\delta}{2}]} f(u) > 0.
\end{aligned}
$$

Case (ii) If $\rho(\zeta) > 1 - \frac{\delta}{2}$, it is easy to verify that $v^-(x,t) \in [x^* + \frac{\delta}{2}, 1-\delta]$. By a similar analysis, we get

$$
\begin{aligned}
&D\frac{\partial v^-(t,x)}{\partial x^2} - \frac{\partial v^-(t,x)}{\partial t} + F(v^-(t,x)\\
\geq &- D\varepsilon^2 - \varepsilon - p\tau\varepsilon + \min_{u\in[x^*+\frac{\delta}{2},1-\delta]} f(u) > 0.
\end{aligned}
$$

Case (iii) If $\rho(\zeta) \in [\frac{\delta}{2}, 1-\frac{\delta}{2}]$, we have

$$
\begin{aligned}
&D\frac{\partial v^-(t,x)}{\partial x^2} - \frac{\partial v^-(t,x)}{\partial t} + F(v^-(t,x))\\
\geq &- D\varepsilon^2 + C\varepsilon[1-(1-x^*)e^{\varepsilon\tau}]\rho'(\zeta) - \varepsilon - p\tau\varepsilon + \min_{u\in[-\delta,1-\delta]} f(u)\\
\geq &- D\varepsilon^2 + C\varepsilon[1-(1-x^*)e^{\varepsilon\tau}]\min_{\rho(\zeta)\in[\frac{\delta}{2},1-\frac{\delta}{2}]} \rho'(\zeta) - \varepsilon - p\tau\varepsilon + \min_{u\in[-\delta,1-\delta]} f(u)\\
> &0.
\end{aligned}
$$

Therefore, v^- is a lower solution of (3.28). Similarly, we can verify that v^+ is an upper solution of (3.28) on $[0,\infty)$. □

In view of Lemma 3.4.1, for any $\eta \in \mathbb{R}$ and $\delta \in [0,\infty)$, we define $w^{\pm}(t,x,\eta,\delta)$ by

$$w^{\pm}(t,x,\eta,\delta) = U(x-ct+\eta \pm \sigma_0\delta(1-e^{-\beta_0 t})) \pm \delta e^{-\beta_0 t},\ \forall x \in \mathbb{R},\ t \in [-\tau,\infty),$$

where σ_0 and β_0 are as in Lemma 3.4.1 and β_0 is chosen small such that $3e^{\beta_0\tau} < 4$. Thanks to Lemmas 3.4.1 and 3.4.2, we can do similar analysis and get the following result. The details of the proof are omitted here since they are essentially the same as those in [54, Lemma 3.2].

Lemma 3.4.3. *Let $U(x-ct)$ be a monotone traveling wave of the system* (3.28), *and $\varphi \in [0,1]_C$ be given such that*

$$\liminf_{x\to\infty} \min_{s\in[-\tau,0]} \varphi(x,s) > x^* \tag{3.32}$$

$$\limsup_{x\to-\infty} \max_{s\in[-\tau,0]} \varphi(x,s) < x^*. \tag{3.33}$$

Then, for any $\delta > 0$, there exists $T > 0, \xi \in \mathbb{R}$ and $h > 0$ such that

$$w_0^-(x,-cT+\xi,\delta)(s) \le u_T(x,\varphi)(s) \le w_0^+(x,-cT+\xi+h,\delta)(s) \tag{3.34}$$

for all $s \in [-\tau,0]$ and $x \in \mathbb{R}$.

By Lemma 3.2.1, system (3.28) admits the comparison principle. In order to get the global stability of traveling waves, we need the following stronger comparison principle.

Lemma 3.4.4. *For any pair of upper solution $\overline{u}(x,t)$ and lower solutions $\underline{u}(t,x)$ of system* (3.28) *on $[0,\infty)$ with $-\delta^* \le \underline{u}(t,x), \overline{u}(x,xt) \le 1+\delta^*$. If $\overline{u}(s,x) \ge \underline{u}(s,x)$ for* *all $s \in [-\tau, 0]$, then there exists a function $\theta(J,t) \in C([0,\infty) \times (0,\infty), \mathbb{R})$ such that the following inequalities hold:*

$$\overline{u}(t,x) - \underline{u}(t,x) \geq \theta(J, t-t_0) \int_z^{z+1} (\overline{u}(t_0,y) - \underline{u}(t_0,y))dy$$

for all $t \geq 0$ and $x \in \mathbb{R}$.

Proof. Let $\tilde{u}(t,x) = \overline{u}(t,x) - \underline{u}(t,x)$. Then Lemma 3.2.1 implies that $\tilde{u}(t,x) \geq 0$ for all $t \in [-\tau, \infty)$ and $x \in \mathbb{R}$. For any given $t_0 > 0$, by (3.5) and definition of upper and lower solutions, we have

$$\begin{aligned}
\tilde{u}(t,x) \geq & T(t-t_0)\tilde{u}(t_0,\cdot)(x) + \int_{t_0}^{t} T(t-r)(F(\underline{u}_r)(x) - F(\overline{u}_r))(x)dr \\
\geq & T(t-t_0)\tilde{u}((t_0,\cdot))(x) + \int_{t_0}^{t} T(t-r)[-p\tilde{u}(r,x) + f(\overline{u}(r,x)) - f(\underline{u}(r,x))]dr \\
\geq & T(t-t_0)\tilde{u}((t_0,\cdot))(x) - L^* \int_{t_0}^{t} T(t-r)\tilde{u}(r,x)dr,
\end{aligned}$$

where $L^* = p + \max_{u \in [-\delta^*, 1+\delta^*]} f'(u) > 0$. Let

$$z(t,x) = e^{-L^*(t-t_0)} T(t-t_0)\tilde{u}(t_0,x), \ t \geq t_0.$$

Then $z(t,x)$ is the solution of the following reaction-diffusion equation:

$$\frac{\partial u(t,x)}{\partial t} = D\frac{\partial^2 u(t,x)}{\partial x^2} - L^* u(t,x).$$

Thus,

$$z(t,x) = T(t-t_0)z(t_0,x) - L^* \int_{t_0}^{t} T(t-r)z(r,x))dr, \ t \geq t_0.$$

By [41, Proposition 3], it follows that $\tilde{u}(t,x) \geq z(t,x)$ for all $t \geq t_0$ and $x \in \mathbb{R}$. Define the function $\theta(J,t) \in C([0,\infty) \times (0,\infty), \mathbb{R})$ by

$$\theta(J,t) = \frac{1}{\sqrt{4D\pi t}} \exp\left(-L^* t - \frac{(J+1)^2}{4Dt}\right), \; J \geq 0, \; t > 0.$$

Then we obtain

$$\begin{aligned}
\tilde{u}(t,x) \geq & e^{-L^*(t-t_0)} T(t-t_0) \tilde{u}(t_0,x) \\
\geq & \frac{e^{-L^*(t-t_0)}}{\sqrt{4D\pi(t-t_0)}} \int_{-\infty}^{\infty} \exp\left(-\frac{(x-y)^2}{4D(t-t_0)}\right) \tilde{u}(t_0,y)dy \\
\geq & \frac{e^{-L^*(t-t_0)}}{\sqrt{4D\pi(t-t_0)}} \int_{z}^{z+1} \exp\left(-\frac{(x-y)^2}{4D(t-t_0)}\right) \tilde{u}(t_0,y)dy \\
\geq & \theta(J, t-t_0) \int_{z}^{z+1} \tilde{u}(t_0,y)dy
\end{aligned} \tag{3.35}$$

for all $x \in \mathbb{R}$ with $|x - z| \leq J$ and $t > t_0 \geq 0$. □

By the stronger comparison principle in Lemma 3.4.4, we have the following result, whose proof is omitted here since it is similar to that of [54, Lemma 3.1].

Lemma 3.4.5. *Let $U(x-ct)$ be a monotone traveling wave solution of system* (3.28). *Then there exists a positive number ϵ^* such that, if $u(t,x)$ is a solution of* (3.28) *on* $[0,\infty)$ *with $0 \leq u(t,x) \leq 1$ for $x \in \mathbb{R}$ and $t \in [0,\infty)$, and* (3.34) *holds for some $\xi \in \mathbb{R}$, $h > 0$, $\delta \in (0, \min(\bar{\delta}, \frac{1}{\sigma_0}))$ and $T > 0$, then for any $t \geq T + \tau + 1$, there exist $\hat{\xi}(t)$, $\hat{\delta}(t)$, and $\hat{h}(t)$ such that*

$$w_0^-(x, -ct + \hat{\xi}(t), \hat{\delta}(t))(s) \leq u_t(x,\varphi)(s) \leq w_0^+(x, -ct + \hat{\xi}(t) + \hat{h}(t), \hat{\delta}(t))(s) \tag{3.36}$$

for all $s \in [-\tau, 0]$, $x \in \mathbb{R}$, *and* $\hat{\xi}(t)$, $\hat{\delta}(t)$, $\hat{h}(t)$ *satisfying*

$$\begin{aligned} \hat{\xi}(t) \in &[\xi - \sigma_0\delta - 2\sigma_0(\delta + \epsilon^* \min(h, 1))e^{\beta_0\tau}, \xi + h + \sigma_0\delta], \\ \hat{\delta}(t) = &(\delta e^{-\beta_0} + \epsilon^* \min(h, 1))e^{-\beta_0(t-(T+\tau+1))}, \\ \hat{h}(t) \in &[0, h + (3e^{\beta_0\tau} - 4)\sigma_0\epsilon^* \min(h, 1) + 3e^{\beta_0\tau}\sigma_0\delta]. \end{aligned} \tag{3.37}$$

By using Lemmas 3.4.3 and 3.4.5, the squeezing technique, which was introduced in [6], and the arguments similar to those in [54, Theorems 3.3–3.4], we can prove the following result on the global stability and uniqueness of bistable waves for system (3.28).

Theorem 3.4.1. *Assume* $U(x - ct)$ *is a monotone traveling wave solution of system* (3.28). *Then* $U(x - ct)$ *is globally asymptotically stable with phase shift in the sense that there exists* $k > 0$ *such that for any* $\varphi \in [0, 1]_c$ *satisfying* (3.32) *and* (3.33), *the solution* $u(t, x, \varphi)$ *of* (3.28) *satisfies*

$$|u(t, x, \varphi) - U(x - ct + \xi)| \le Ke^{-kt}, \quad \forall x \in \mathbb{R},\, t \ge 0$$

for some $K = K(\varphi) > 0$ *and* $\xi = \xi(\varphi) \in \mathbb{R}$. *Moreover,* $U(x - ct)$ *is unique up to a translation in the sense that for any traveling wave solution* $\bar{U}(x - \bar{c}t)$ *with* $0 \le \bar{U}(\xi) \le 1$, $\xi \in \mathbb{R}$, *we have* $\bar{c} = c$ *and* $\bar{U}(\cdot) = U(\xi_0 + \cdot)$ *for some* $\xi_0 \in \mathbb{R}$.

Chapter 4

A Reaction-Diffusion Model with Seasonal Succession

4.1 Introduction

Seasonal succession is a very natural phenomenon which is important for the growth and survival of species. Due to the seasonal alternate, populations experience a periodic dynamical environment such as temperature, rainfall, humidity and wind. For example, in temperate lakes there is a growing season for the phytoplankton and zooplankton during warms months after which species die off or form resting stages in the winter. The environmental variation leads to a regular succession of species over the seasons, called seasonal succession. It has been a fascinating subject for ecologists and mathematicians to study the dynamics of periodic models by means of seasonal succession numerically and analytically. Litchman and Klausmeimer [31] studied a competition model of two species for a single nutrient under fluctuating light with season succession in the chemostat. In [55], Steiner et al. employed a novel approach to model a seasonally forced predator-prey system, and gave some experimental data about the effect of the seasonal succession to predict the competition of phytoplankton species. Recently, Gourley, Liu and Wu [14] presented a patch model to describe seasonal evolution of migratory birds and obtained a threshold type result on its global dynamics. For more research works on the seasonal succession, we refer to [10, 24, 22, 46] and references therein.

More recently, Hsu and Zhao [22] studied the global dynamics of the following Lotka-Volterra competition model with seasonal succession:

$$\begin{aligned}
&\frac{du_i}{dt} = -\lambda_i u_i, \;\; m\omega \le t \le m\omega + (1-\phi)\omega, \;\; i = 1, 2,\\
&\frac{du_1}{dt} = r_1 u_1[1 - \frac{u_1}{K_1}] - \alpha u_1 u_2, \;\; m\omega + (1-\phi)\omega \le t \le (m+1)\omega,\\
&\frac{du_2}{dt} = r_2 u_2[1 - \frac{u_2}{K_2}] - \beta u_1 u_2, \;\; m\omega + (1-\phi)\omega \le t \le (m+1)\omega,\\
&(u_1(0), u_2(0)) = u_0 \in \mathbb{R}^2_+,
\end{aligned} \tag{4.1}$$

where $m \in \mathbb{Z}_+, \lambda_i, r_i, K_i, \alpha$ and β are all positive constants, and $\phi \in (0, 1]$. The authors gave a complete classification for the global dynamics of (4.1) in terms of parameters via the stability analysis of equilibria and theory of monotone dynamical systems. According to [22, Theorem 2.4], system (4.1) admits a saddle-point structure provided the parameters satisfy the following conditions:

(c1) $r_i\phi - \lambda_i(1-\phi) > 0, \;\; i = 1, 2.$

(c2) $r_1\phi - \lambda_1(1-\phi) < \frac{\alpha K_2}{r_2}(r_2\phi - \lambda_2(1-\phi)).$

(c3) $r_2\phi - \lambda_2(1-\phi) < \frac{\beta K_1}{r_1}(r_1\phi - \lambda_1(1-\phi)).$

Note that the existence, uniqueness, and stability of ω-periodic solutions of a periodic evolution system are equivalent to those of fixed points of its Poincaré (period) map. Thus, [22, Theorem 2.4] implies that the Poincaré map associated with (4.1) has a trivial unstable fixed point $(0, 0)$ and a unique positive fixed point $\bar{u} = (\bar{u}_1, \bar{u}_2)$ (saddle point) between two stable semitrivial fixed points $(0, u_2^*)$ and $(u_1^*, 0)$. Furthermore, there exists a continuous, unbounded and one-dimensional curve $\Gamma \subset \mathbb{R}_+^2$ such that both fixed points $(0,0)$ and $\bar{u}$ are in Γ, and all solutions of system (4.1) with initial date below Γ are asymptotic to $(u_1^*(t), 0)$, and all solutions of system (4.1) with initial data above Γ are asymptotic to $(0, u_2^*(t))$, while all solutions of system (4.1) with initial date $u^0 \in \Gamma\backslash\{0\}$ are asymptotic to $\bar{u}(t)$, where $(0, u_2^*(t))$, $(u_1^*(t), 0)$ and $\bar{u}(t)$ are the ω-periodic solutions of system (4.1) with the initial data $(0, u_2^*)$, $(u_1^*, 0)$ and $\bar{u}$, respectively.

In this chapter, we consider the following reaction-diffusion competition model with seasonal succession:

$$
\begin{aligned}
&\frac{\partial u_i}{\partial t} = -\lambda_i u_i, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \; i = 1, 2, \\
&\frac{\partial u_1}{\partial t} = d_1 \Delta u_1 + r_1 u_1 [1 - \frac{u_1}{K_1}] - \alpha u_1 u_2, \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega \\
&\frac{\partial u_2}{\partial t} = d_2 \Delta u_2 + r_2 u_2 [1 - \frac{u_2}{K_2}] - \beta u_1 u_2, \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \\
&(u_1(0,\cdot), u_2(0,\cdot)) = u_0 \in C(\mathbb{R}, \mathbb{R}_+^2),
\end{aligned}
\tag{4.2}
$$

where d_1 and d_2 are positive constants. We assume that all parameters satisfy (c1)-(c3) so that the spatially homogeneous system (4.1) admits a bistable dynamics. Here we are interested in the existence of ω-periodic bistable traveling wave solutions of (4.2) connecting $(0, u_2^*(t))$ to $(u_1^*(t), 0)$, and their global stability with phase shift. It is worthy to mention Alikakos, Bates and Chen's work [1] on bistable waves for scalar periodic reaction-diffusion equations, and Shen's work [50, 51] on bistable waves for scalar almost periodic reaction-diffusion equations. We will use a different approach to study bistable traveling waves for system (4.2). More precisely, we prove the existence of periodic bistable waves by appealing to the theory of bistable waves recently developed in [13] for monotone semiflows, which allows the presence of multiple intermediate unstable fixed points in between two stable ones. We further employ the global convergence result Theorem 1.1.2 to establish the global stability of such a periodic traveling wave.

The rest of this chapter is organized as follows. In section 4.2, we establish the existence of ω-periodic bistable traveling waves by verifying abstract assumptions in [13]. In section 4.3, we use the above mentioned convergence theorem and the method of upper and lower solutions to prove the global stability of traveling waves and their uniqueness up to translation. In section 4.4, we present some numerical simulations to illustrate our analytic results.

4.2 Periodic traveling waves

In this section, we establish the existence of periodic bistable traveling waves for system (4.2).

Recall that $U(t, x - ct)$ is said to be an ω-time periodic traveling wave of the semiflow $\{Q_t\}_{t\geq 0}$ if $Q_t[U(0,\cdot)](x) = U(t, x - ct)$ and $U(t,x) = U(t+\omega, x)$ for all $t \geq 0, x \in \mathbb{R}$. As usual, we call c the wave speed, and $U(t,z)$ the wave profile.

Let $\mathcal{C}$, $\mathcal{C}_+$, $\mathcal{C}_r$, and $[a,b]_{\mathcal{C}}$ be defined as in Section 2.2. For the convenience of mathematical analysis, we make a change of variables

$$u_1 = v_1, \;\; u_2 = -v_2,$$

which converts system (4.2) into the following cooperative system:

$$\begin{aligned}
&\frac{\partial v_i}{\partial t} = -\lambda_i v_i, \ \ m\omega \le t \le m\omega + (1-\phi)\omega, \ \ i = 1, 2, \\
&\frac{\partial v_1}{\partial t} = d_1 \Delta v_1 + r_1 v_1 [1 - \frac{v_1}{K_1}] + \alpha v_1 v_2, \ \ m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \\
&\frac{\partial v_2}{\partial t} = d_2 \Delta v_2 + r_2 v_2 [1 + \frac{v_2}{K_2}] - \beta v_1 v_2, \ \ m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \\
&(v_1(0,\cdot), v_2(0,\cdot)) = v_0(\cdot) \in C(\mathbb{R}, \mathbb{R}_+ \times \mathbb{R}_-).
\end{aligned} \tag{4.3}$$

It is easy to see that the Poincaré map of system (4.3) has four fixed points: $E^0 = (0,0)$, $E^1 = (0, v_2^*)$, $E^2 = (v_1^*, 0)$, and $E^3 = (\bar{v}_1, \bar{v}_2)$, where $v_2^* = -u_2^*$, $v_1^* = u_1^*$, and $(\bar{v}_1, \bar{v}_2) = (\bar{u}_1, -\bar{u}_2)$. Note that (4.3) is order preserving in the relevant range $[E^1, E^2]_C$. Then the existence of the time-periodic traveling waves connecting two stable periodic solutions $(0, u_2^*(t))$ and $(u_1^*(t), 0)$ for system (4.2) is equivalent to that of traveling waves connecting two stable periodic solutions $V^-(t) := (0, v_2^*(t))$ and $V^+(t) := (v_1^*(t), 0)$ for system (4.3). Thus, it suffices to analyze system (4.3) to get the corresponding dynamical behaviors of model (4.2). In what follows, we focus on the global dynamics of the monotone system (4.3).

Let $\{\Phi_t\}_{t\ge 0}$ be the solution semiflow associated with (4.3), that is, $\Phi_t(v_0)$, as a function of t, is the unique global solution of system (4.3) on $[0, +\infty)$. For convenience, we use S to denote the Poincaré map Φ_ω.

Lemma 4.2.1. *Let $E = \{E^0, E^1, E^2, E^3\}$. Then the map S satisfies (C1)-(C6) in section 1.2.2 with 0, β and $\mathcal{C}_\beta$ replaced by E^1, E^2 and $[E^1, E^2]_C$, respectively.*

Proof. It is easy to see that S satisfies (C1)-(C4). In what follows, we only verify (C5) and (C6).

Let $\widehat{S}$ be the restriction of S to $[E^1, E^2] \subset \mathbb{R}^2$. Then $\widehat{S}$ has four fixed points $E^i, i = 0, 1, 2, 3$, and we need to show that the fixed point E^1 is stable from above and E^2 is stable from below. From the proof of [22, Lemma 2.3], it is easy to see that the Jacobian matrices of $\widehat{S}$ at E^1 and E^2 are

$$D\hat{S}(E^1) = \begin{pmatrix} e^{-(r_1\phi-\lambda_1(1-\phi))\omega} & a_1 \\ 0 & e^{(r_2\phi-\lambda_2(1-\phi)-\frac{\beta K_1}{r_1}(r_1\phi-\lambda_1(1-\phi)))\omega} \end{pmatrix},$$

and

$$D\hat{S}(E^2) = \begin{pmatrix} e^{-(r_2\phi-\lambda_2(1-\phi))\omega} & a_2 \\ 0 & e^{(r_1\phi-\lambda_1(1-\phi)-\frac{\beta K_2}{r_2}(r_2\phi-\lambda_2(1-\phi)))\omega} \end{pmatrix},$$

where a_1 and a_2 are positive constants due to the fact that system (4.3) is cooperative. Clearly, $D\hat{S}(E^1)$ has two positive eigenvalues $\lambda_1 = e^{-(r_1\phi-\lambda_1(1-\phi))\omega} < 1$ and $\lambda_2 = e^{(r_2\phi-\lambda_2(1-\phi)-\frac{\beta K_1}{r_1}(r_1\phi-\lambda_1(1-\phi)))\omega} < 1$. If $\lambda_1 < \lambda_2$, then $D\hat{S}(E^1)$ admits an unit eigenvector $e_0 \gg 0$ associated with λ_2 such that

$$D\hat{S}(E^1)(e_0) = \lambda_2 e_0 \ll e_0.$$

If $\lambda_2 \leq \lambda_1$, we choose $k \in (\lambda_1, 1), \varepsilon_0 \in \left(0, \frac{k-\lambda_1}{a_1}\right)$, and $e_0 = \left(\frac{1}{\sqrt{1+\varepsilon_0^2}}, \frac{\varepsilon_0}{\sqrt{1+\varepsilon_0^2}}\right)^T \gg 0$ such that

$$D\hat{S}(E^1)(e_0) \ll ke_0 \ll e_0.$$

By the continuous differentiability of $\widehat{S}$, it then follows that there exists $\delta > 0$ such that

$$\begin{aligned} \widehat{S}(E^1 + \eta e_0) =& \widehat{S}(E^1) + \int_0^1 D\widehat{S}(E^1 + t\eta e_0)\eta e_0 dt \\ =& E^1 + \eta \int_0^1 D\widehat{S}(E^1 + t\eta e_0) e_0 dt \\ \leq& E^1 + \eta k e_0 \ll E^1 + \eta e_0 \end{aligned}$$

for all $\eta \in (0, \delta]$, and hence, E^1 is strongly stable from above for the map $\widehat{S}$. A similar argument shows that E^2 is strongly stable from below.

In order to estimate the spreading speed $c^*(E^0, E^1)$, we only need to consider the following subsystem of (4.3):

$$\begin{aligned} \frac{\partial v_1}{\partial t} &= -\lambda_1 v_1, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \\ \frac{\partial v_1}{\partial t} &= d_1 \Delta v_1 + r_1 v_1 [1 - \frac{v_1}{K_1}], \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \end{aligned} \tag{4.4}$$

From [46, Theorem 4.5], we have

$$c^*(E^0, E^1) = 2\sqrt{d\phi(r_1\phi - \lambda_1(1-\phi))} > 0.$$

A similar argument shows that the spreading speed

$$c^*(E^0, E^2) = 2\sqrt{d\phi(r_2\phi - \lambda_2(1-\phi))} > 0.$$

Then we have $c^*(E^0, E^1) + c^*(E^0, E^2) > 0$.

For notational convenience, we define $F = (F_1, F_2)^T$ as

$$F_1(v_1, v_2) = r_1 v_1 [1 - \frac{v_1}{K_1}] + \alpha v_1 v_2,$$

$$F_2(v_1, v_2) = r_2 v_2 [1 + \frac{v_2}{K_2}] - \beta v_1 v_2.$$

In order to estimate $c^*(E^3, E^2)$, letting $V(t) = U(t) + \bar{V}(t)$ in system (4.3), we then see that U satisfies the following system:

$$\begin{aligned} \frac{\partial U}{\partial t} &= -\Lambda U, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \\ \frac{\partial U}{\partial t} &= DU_{xx} + F(U + \bar{V}(t)) - F(\bar{V}(t)), \quad m\omega + (1-\phi)\omega \le t \le (m+1)\omega, \end{aligned} \tag{4.5}$$

where $U := (u_1, u_2)^T$, $V := (v_1, v_2)^T$, $\bar{V}(t) := (\bar{v}_1(t), \bar{v}_2(t))^T$, $\Lambda := diag(\lambda_1, \lambda_2)$, $D := diag(d_1, d_2)$. Let $\{\Psi_t\}_{t \ge 0}$ be solution semiflow determined by (4.5). Then it easily follows that $\Phi_t(\cdot) = \Psi_t(\cdot - E^3) + \bar{V}(t)$. In particular, letting $t = \omega$, we have $\Phi_\omega(\cdot) = \Psi_\omega(\cdot - E^3) + E^3$. Thus, Φ_ω satisfies conditions (A1)-(A5) with fixed points $E^3 \ll E^2$ if and only if so does Ψ_ω with fixed points $0 \ll E^2 - E^3$. From Theorem 1.2.4 with $Q := \Phi_\omega$ and $Q := \Psi_\omega$, respectively, it is easy to see that $c^*(E^3, E^2) = c^*_\Psi(0, E^2 - E^3)$, where $c^*_\Psi(0, E^2 - E^3)$ is the asymptotic speed of spread determined by Ψ_ω with fixed points 0 and $E^2 - E^3$.

Now we prove $c^*_\Psi(0, E^2 - E^3) > 0$. To estimate $c^*_\Psi(0, E^2 - E^3)$, we consider the following linear system:

$$\begin{aligned} \frac{\partial U}{\partial t} &= -\Lambda U, \;\; m\omega \leq t \leq m\omega + (1-\phi)\omega, \\ \frac{\partial U}{\partial t} &= DU_{xx} + D_u F(\bar{V}(t))U, \;\; m\omega + (1-\phi)\omega \leq t \leq (m+1)\omega, \end{aligned} \tag{4.6}$$

where

$$D_v F(\bar{V}(t)) = \begin{pmatrix} r_1[1 - \frac{2\bar{v}_1(t)}{K_1}] + \alpha \bar{v}_2(t) & \alpha \bar{v}_1(t) \\ -\beta \bar{v}_2(t) & r_2[1 + \frac{2\bar{v}_2(t)}{K_2}] - \beta \bar{v}_1(t) \end{pmatrix}$$

is the Jacobian matrix of F at $\bar{V}(t)$. Let $\{M_t\}_{t \geq 0}$ be the solution semiflow determined by (4.6), that is, for any $U_0 \in \mathcal{C}$, $M_t(U_0)$ is the unique solution of (4.6) on $[0, \infty)$.

Note that two off-diagonal entries of $D_v F(\bar{V}(t))$ are positive for any $t \in [0, \omega]$. Choose $\rho > 0$ such that $D_v F(\bar{V}(t)) + \rho I$ is strictly positive, that is, all entries are positive. Define

$$\sigma = \min_{t \in [0,\omega]} \left\{ \frac{\partial F_i}{\partial u_j}(\bar{V}(t)) + \rho \delta_i^j, i, j = 1, 2 \right\} > 0.$$

Then for any $\varepsilon > 0$, there exists $\eta \gg 0$ such that

$$F(U + \bar{V}(t)) - F(\bar{V}(t)) \geq D_u F(\bar{V}(t))U - \bar{\varepsilon}\sigma \|U\|$$

holds for any $U \in [0,\eta]_C$, where $\vec{\varepsilon} = (\varepsilon,\varepsilon)^T$. Since

$$\|U\| \leq U_1 + U_2 \leq \sigma^{-1}(D_uF(\bar{V}(t))U + \rho U)_i, i = 1,2, \forall U \geq 0,$$

it follows that

$$F(U + \bar{V}(t)) - F(\bar{V}(t)) \geq D_uF(\bar{V}(t))U - \varepsilon(D_uF(\bar{V}(t)) + \rho I)U. \tag{4.7}$$

Let $\{M_t^\varepsilon\}_{t\geq 0}$ be the solution semiflow associated with the following linear periodic system:

$$\begin{aligned}
\frac{\partial U}{\partial t} &= -\Lambda U, \ \ m\omega \leq t \leq m\omega + (1-\phi)\omega, \\
\frac{\partial U}{\partial t} &= DU_{xx} + D_uF(\bar{V}(t))U - \varepsilon(D_uF(\bar{V}(t)) + \rho I)U, \\
&\quad m\omega + (1-\phi)\omega \leq t \leq (m+1)\omega.
\end{aligned} \tag{4.8}$$

Let $U(t,\varrho)$ be the solution of spatially homogeneous system of (4.5) with $U(0,\varrho) = \varrho$. By the continuity of solutions with initial data, it follows that for $\eta \gg 0$, there exists $\varrho = \varrho(\varepsilon) \gg 0$ in $\mathbb{R}^2$ such that

$$U(t,\varrho) \leq \eta, \forall t \in [0,\omega].$$

By the comparison principle, we have

$$\Psi_t(\psi) \leq \Psi_t(\varrho) = U(t,\varrho) \leq \eta, \forall \psi \in [0,\varrho]_C, t \in [0,\omega].$$

Combining (4.7), we further get

$$\Psi_t(\psi) \geq M_t^\varepsilon(\psi), \forall \psi \in [0,\varrho]_C, t \in [0,\omega]. \tag{4.9}$$

Let $U(t,x)=e^{-\mu x}\Gamma(t)$ be the solution of (4.8), where $\Gamma(t)=(\gamma_1(t),\gamma_2(t))^T$. Then $\Gamma(t)$ satisfies the following equations

$$
\begin{aligned}
\frac{d\Gamma}{dt} &= -\Lambda\Gamma, \quad m\omega \le t \le m\omega+(1-\phi)\omega, \\
\frac{d\Gamma}{dt} &= [D\mu^2+D_uF(\bar{V}(t))]\Gamma-\varepsilon(D_uF(\bar{V}(t))+\rho I)\Gamma, \\
& \quad m\omega+(1-\phi)\omega \le t \le (m+1)\omega.
\end{aligned}
\tag{4.10}
$$

Let $\rho_\varepsilon(\mu)$ be the principle Floquet multiplier of (4.10). Then $\rho_0(0)>1$ due to the fact that $\bar{V}(t)$ is unstable. Since $\lim\limits_{\varepsilon\to 0^+}\rho_\varepsilon(0)=\rho_0(0)$, we can fix an $\varepsilon\in(0,1)$ such that $\rho_\varepsilon(0)>1$. It is easy to see that if $\Gamma(t,\Gamma_0)$ is a solution of (4.10) satisfying $\Gamma(0,\Gamma_0)=\Gamma_0\in\mathbb{R}^2$, then $U(t,x)=e^{-\mu x}\Gamma(t,x)$ is a solution of linear periodic system (4.8). Define $\Psi_\varepsilon(\mu):=\frac{\ln\rho_\varepsilon(\mu)}{\mu}$. By Theorem 1.2.2 and inequality (4.9), we have

$$
c^*(E^3,E^2)=c^*_\Psi(0,E^2-E^3)\ge\inf_{\mu>0}\Psi_\varepsilon(\mu).
$$

Now we need to verify $\Psi_\varepsilon(+\infty)=+\infty$. Let $\lambda_\varepsilon(\mu)=\frac{\ln\rho_\varepsilon(\mu)}{\omega}$. By the Floquet theory, there exists a positive ω-periodic function $\xi(t):=(\xi_1(t),\xi_2(t))^T$ such that $\Gamma(t):=e^{\lambda_\varepsilon(\mu)t}\xi(t)$ is a solution of (4.10). Then we have

$$
\begin{aligned}
\xi'(t) &=[-\Lambda-\lambda_\varepsilon(\mu)I]\xi(t), \quad m\omega\le t\le m\omega+(1-\phi)\omega, \\
\xi'(t) &= [D\mu^2-\lambda_\varepsilon(\mu)I-\varepsilon\rho I]\xi(t)+(1-\varepsilon)D_uF(\bar{V}(t))]\xi(t), \\
& \quad m\omega+(1-\phi)\omega\le t\le(m+1)\omega.
\end{aligned}
\tag{4.11}
$$

It easily follows that

$$\begin{aligned}\frac{\xi_1'(t)}{\xi_1(t)} =&[-\lambda_1 - \lambda_\varepsilon(\mu)], \quad m\omega \le t \le m\omega + (1-\phi)\omega,\\ \frac{\xi_1'(t)}{\xi_1(t)} =& [d_1\mu^2 - \lambda_\varepsilon(\mu) - \varepsilon\rho] + (1-\varepsilon)[F_{11}(\bar{V}(t))\xi_1 + F_{12}(\bar{V}(t))\xi_2]/\xi_1,\\ & m\omega + (1-\phi)\omega \le t \le (m+1)\omega.\end{aligned} \tag{4.12}$$

Integrating the above equation from 0 to ω, we get

$$\begin{aligned}0 =& \int_0^{(1-\phi)\omega} (-\lambda_1 - \lambda_\varepsilon(\mu))dt + \int_{(1-\phi)\omega}^{\omega} (d_1\mu^2 - \lambda_\varepsilon(\mu) - \varepsilon\rho)dt\\ &+(1-\varepsilon)\int_{(1-\phi)\omega}^{\omega} (F_{11}(\bar{V}(t)) + F_{12}(\bar{V}(t))\xi_2/\xi_1)dt,\end{aligned} \tag{4.13}$$

and hence,

$$0 \ge -\lambda_1(1-\phi)\omega - \lambda_\varepsilon(\mu)\omega + d_1\mu^2\omega\phi - \varepsilon\rho\phi\omega + (1-\varepsilon)\int_{(1-\phi)\omega}^{\omega} F_{11}(\bar{V}(t))dt.$$

Then we obtain

$$\Psi_\varepsilon(\mu) = \frac{\omega\lambda_\varepsilon(\mu)}{\mu} \ge d_1\mu\omega\phi + \frac{-\lambda_1(1-\phi)\omega - \varepsilon\rho\phi\omega + (1-\varepsilon)\int_{(1-\phi)\omega}^{\omega} F_{11}(\bar{V}(t))dt}{\mu},$$

which implies that $\Psi_\varepsilon(+\infty) = +\infty$. By Lemma 1.2.1, we have $\inf\limits_{\mu>0} \Psi_\varepsilon(\mu) > 0$. It then follows that

$$c^*(E^3, E^2) = c^*_\Psi(0, E^2 - E^3) \ge \inf_{\mu>0} \Psi_\varepsilon(\mu) > 0.$$

In order to estimate $c^*(E^3, E^1)$, we let $V(t) = \bar{V}(t) - U(t)$ in system (4.3). By a similar argument as we did above, we can show that $c^*(E^3, E^1) > 0$. Thus, condition (C6) holds with $Q := S$. $\square$

By Theorem 1.2.7 and Lemma 4.2.1, we have the following result.

Theorem 4.2.1. *Let all parameters satisfy (c1)-(c3). Then there exists $c \in \mathbb{R}$ such that the cooperative system* (4.3), *which is obtained by making substitution $u_1 = v_1, u_2 = -v_2$ in model* (4.2), *has a time-periodic traveling wave $V(t, x - ct)$ with $V(t, -\infty) = (0, v_2^*(t))$ and $V(t, +\infty) = (v_1^*(t), 0)$ uniformly for $t \in \mathbb{R}$. Furthermore, $V(t, z)$ is nondecreasing in $z \in \mathbb{R}$.*

To finish this section, we remark that when $\phi = 1$, system (4.2) becomes an autonomous two species Lotka-Volterra competition model. Thus, the existence of bistable traveling waves is implied by Theorem 1.1 in [58, Chapter 3], as applied to the cooperative system (4.3) with $\phi = 1$.

4.3 Global stability

In this section, we investigate the global stability and uniqueness of periodic traveling waves for system (4.3).

Let $\mathcal{X} = BUC(\mathbb{R}, \mathbb{R}^2)$ be the Banach space of all bounded and uniformly continuous functions from $\mathbb{R}$ to $\mathbb{R}^2$ with the usual supreme norm. Let $\mathcal{X}_+ = \{(\psi_1, \psi_2) \in \mathcal{X} : \psi_i(x) \geq 0, \forall x \in \mathbb{R}, i = 1, 2\}$. Then $\mathcal{X}_+$ is a closed cone of $\mathcal{X}$ and its induced partial ordering makes $\mathcal{X}$ into a Banach lattice. In what follows, we denote

$$\mathcal{S} := \{(\psi_1, \psi_2) \in \mathcal{X} : \psi_1(x) \geq 0, \psi_2(x) \leq 0, \forall x \in \mathbb{R}\}.$$

Let $V(t, x - ct) = (v_1(t, x - ct), v_2(t, x - ct))$ be a traveling wave solution of (4.3) connecting $(0, v_2^*(t))$ to $(v_1^*(t), 0)$. By using coordinate $z = x - ct$, we transform (4.3) into the following system:

$$
\begin{aligned}
\frac{\partial v_i}{\partial t} &= c\frac{\partial v_i}{\partial z} - \lambda_i v_i, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \\
\frac{\partial v_i}{\partial t} &= d_i\frac{\partial^2 v_i}{\partial z^2} + c\frac{\partial v_i}{\partial z} + F_i(v_1, v_2), \; m\omega + (1-\phi)\omega \le t \le (m+1)\omega,
\end{aligned}
\tag{4.14}
$$

where $i = 1, 2$ and c is the speed of the ω-time periodic traveling wave. Thus, $V(t, z)$ is a time-periodic solution of system (4.14). By Theorem 4.2.1 and the strong maximum principle, we further know that $V_z(t, z) > 0$ for all $t \ge 0$ and $x \in \mathbb{R}$. Let $v(t, z, \psi) = (v_1(t, z), v_2(t, z))$ be the solution of (4.14) with initial data $v(0, \cdot, \psi) = \psi \in \mathcal{S}$. Clearly, the solution $\bar{v}(t, x, \psi)$ of (4.3) with initial data ψ is given by $\bar{v}(t, x, \psi) = v(t, x - ct, \psi)$.

We also need the following concept of upper and lower solutions for system (4.14).

Definition 4.3.1. *A function $\tilde{V}(t, z) = (\tilde{V}_1(t, z), \tilde{V}_2(t, z))$ is an upper solution of* (4.14) *if $\tilde{V}(t, z)$ satisfies*

$$
\begin{aligned}
&\frac{\partial \tilde{V}_i}{\partial t} - c\frac{\partial \tilde{V}_i}{\partial z} + \lambda_i v_i \ge 0, \quad m\omega \le t \le m\omega + (1-\phi)\omega, \\
&\frac{\partial \tilde{V}_i}{\partial t} - d_i\frac{\partial^2 \tilde{V}_i}{\partial z^2} - c\frac{\partial \tilde{V}_i}{\partial z} - F_i(\tilde{V}_1, \tilde{V}_2) \ge 0, \; m\omega + (1-\phi)\omega \le t \le (m+1)\omega.
\end{aligned}
$$

Similarly, we can define the lower solution of (4.14) *by reversing above inequalities.*

Lemma 4.3.1. *If $\psi \in \mathcal{S}$ satisfies*

$$
\limsup_{\xi \to -\infty} \psi(\xi) \ll E^3 \ll \liminf_{\xi \to \infty} \psi(\xi), \tag{4.15}
$$

then for any $\varepsilon > 0$, there exist positive number $\tilde{z} = \tilde{z}(\varepsilon, \psi)$ and $\tilde{k} = \tilde{k}(\varepsilon, \psi)$ such that $V(0, z - \tilde{z}) - \vec{\varepsilon} \le v(\tilde{k}\omega, z, \psi) \le V(0, z + \tilde{z}) + \vec{\varepsilon}, \quad \forall z \in \mathbb{R}$.

Proof. Without loss of generality, we assume that $\psi(z) \le l_1, \ \forall z \in \mathbb{R}$ and $\psi(z) \le l_2, \ \forall z \le 0$, where $l_1, \ l_2 \in \mathbb{R}^2, \ l_1 \ge E^2, \ E^1 \le l_2 \ll E^3$. Let $v^+(t) = v(t, 2l_1 - l_2)$,

$v^-(t) = v(t, l_2)$ be the spatially homogeneous solution of (4.14) with the $v^+(0) = 2l_1 - l_2$, $v^-(0) = l_2$. Define $\eta(s) = \frac{1}{2}(1+\tanh(s/2))$. Then $\eta' = \eta(1-\eta)$, $\eta'' = \eta'(1-2\eta)$. Let

$$\begin{aligned}\tilde{c} =& c + d_1 + d_2 + \frac{1}{2}\sup\{\frac{(v_1^+ - v_1^-)^2}{v_i^+ - v_i^-}|F_i^{11}(\theta)| + \frac{(v_2^+ - v_2^-)^2}{v_i^+ - v_i^-}|F_i^{22}(\theta)| + 2(v_j^+ - v_j^-) \\ & |F_i^{12}(\theta)|, t \in [m\omega + (1-\phi)\omega, (m+1)\omega], \theta \in (v^-(t), v^+(t)), 1 \le j \ne i \le 2\},\end{aligned}$$

and $\bar{c} \ge \tilde{c}$ be a fixed number. Define

$$\bar{V}(t, z) = v^+(t)\eta(z + \bar{c}t) + v^-(t)(1 - \eta(z + \bar{c}t)).$$

It is easy to see that $\bar{V}(0, z) \ge \psi(z)$. In order to show that $\bar{V}(t, z)$ is an upper solution of (4.14), we distinguish between two cases:

In the case where $t \in [m\omega, m\omega + (1-\phi)\omega]$, $m \in \mathbb{Z}^+$, we have

$$\begin{aligned}&\frac{\partial \bar{V}_i}{\partial t} - c\frac{\partial \bar{V}_1}{\partial z} + \lambda_i \bar{V}_i \\ =&(v_i^+)'\eta + \bar{c}v_i^+\eta' + (v_i^-)'(1-\eta) - \bar{c}v_i^-\eta' - c(v_i^+\eta' - v_i^-\eta') + \lambda_i(v_i^+\eta - \bar{c}v_i^-\eta') \\ =& -\lambda_i v_i^+\eta + \bar{c}v_i^+\eta' - \lambda_i v_i^-(t)(1-\eta) - \bar{c}v_i^-\eta' - c\eta'(v_i^+ - v_i^-) + \lambda_i(v_i^+\eta + v_i^-(1-\eta)) \\ =&(\bar{c} - c)(v_i^+ - v_i^-)\eta(1-\eta) \ge 0\end{aligned}$$

In the case where $t \in [m\omega + (1-\phi)\omega, (m+1)\omega]$, $m \in \mathbb{Z}^+$, we obtain

$$\begin{aligned}
&\frac{\partial \bar{V}_i}{\partial t} - c\frac{\partial \bar{V}_1}{\partial z} - d_i\frac{\partial^2 \bar{V}_i}{\partial z^2} - F_i(\bar{V}_1, \bar{V}_2) \\
=&(v_i^+)'\eta + \bar{c}v_i^+\eta' + (v_i^-)'(1-\eta) - \bar{c}v_i^-\eta' - c\eta'(v_i^+ - v_i^-) - d_i\eta''(v_i^+ - v_i^-) - F_i(\bar{V}) \\
=&\eta F_i(v^+) + (1-\eta)F_i(v^-) + (\bar{c} - c)\eta'(v_i^+ - v_i^-) - d_i(v_i^+ - v_i^-)\eta'(1-2\eta) - F_i(\bar{V}) \\
=&\eta F_i(v^+) + (1-\eta)F_i(v^-) + \eta(1-\eta)[(\bar{c} - c) - d_i(1-2\eta)](v_i^+ - v_i^-) - F_i(\bar{V}) \\
=&\frac{1}{2}\eta(1-\eta)(v_1^+ - v_1^-)^2F_i^{11}(\theta) + \frac{1}{2}\eta(1-\eta)(v_2^+ - v_2^-)^2F_i^{22}(\theta) + \eta(1-\eta) \\
&(v_1^+ - v_1^-)(v_2^+ - v_2^-)F_i^{12}(\theta) + \eta(1-\eta)[(\bar{c} - c) - d_i(1-2\eta)](v_i^+ - v_i^-) \geq 0.
\end{aligned}$$

Thus, $\bar{V}(t, z)$ is an upper solution of (4.14).

By the comparison principle, we have $v(t, z, \psi) \leq \bar{V}(t, z)$, $\forall t \geq 0$, $z \in \mathbb{R}$. Since $\lim_{k\to+\infty} v^-(k\omega + t) = (0, v_2^*(t))$ and $\lim_{k\to+\infty} v^+(k\omega + t) = (v_1^*(t), 0)$, it follows that for any $\varepsilon > 0$, there exist positive number $\tilde{z} = \tilde{z}(\varepsilon, \psi)$ and $\tilde{k} = \tilde{k}(\varepsilon, \psi)$ such that $v(\tilde{k}\omega, z, \psi) \leq V(0, z + \tilde{z}) + \vec{\varepsilon}$, $\forall z \in \mathbb{R}$. A similar argument for the lower solution completes the proof. □

Lemma 4.3.2. *For any $\psi \in \mathcal{S}$, there exist positive constants ε_0, K_0, ρ_0 such that if for some $\varepsilon \in (0, \varepsilon_0]$ and $\hat{z} \in \mathbb{R}$,*

$$\psi(\cdot) \leq V(0, \cdot + \hat{z}) + \vec{\varepsilon}$$

or

$$\psi(\cdot) \geq V(0, \cdot - \hat{z}) - \vec{\varepsilon},$$

then for all $t \geq 0$,

$$v(t, \cdot, \psi) \leq V(t, \cdot + \hat{z} + K_0\varepsilon) + K_0\vec{\varepsilon}e^{-\rho_0 t}$$

or

$$v(t,\cdot,\psi) \geq V(t,\cdot - \hat{z} - K_0\varepsilon) - K_0\vec{\varepsilon}e^{-\rho_0 t}.$$

Proof. Without loss of generality, we assume that $\hat{z} = 0$. Let $\mu^{\pm} = \frac{1}{\omega}\ln r^{\pm}$, where $r^{\pm}$ are the spectral radius of $DS(E^1)$ and $DS(E^2)$, respectively. From the stability of E^1 and E^2, we know that $\mu^{\pm} < 0$. For the convenience of analysis, we rewrite system (4.14) into the following system

$$\frac{\partial v}{\partial t} = D\frac{\partial^2 v}{\partial z^2} + c\frac{\partial v}{\partial z} + G(v_1, v_2) \tag{4.16}$$

where $D = 0$, $G(v_1, v_2) = (-\lambda_1 v_1, -\lambda_2 v_2)^T$ in bad season ($t \in [m\omega, m\omega + (1-\psi)\omega]$), while $D = diag(d_1, d_2)$, $G(v_1, v_2) = F(v_1, v_2)$ in good season ($t \in [m\omega + (1-\psi)\omega, (m+1)\omega,]$). From [66, Lemma 2.1] and the proof of [22, Lemma 2.3], we see that there exist positive, ω-periodic function $s^{\pm}(t)$ such that $v^{\pm}(t) = e^{\mu^{\pm}t}s^{\pm}(t)$ are the solution of the ω-periodic system

$$v'(t) = DG(V^{\pm}(t))v(t)$$

with the initial data $v^{\pm}(0) \gg \vec{1}$. Let $\nu^{\pm} = -\frac{\mu^{\pm}}{2} > 0$, $a^{\pm}(t) := (a_1^{\pm}(t), a_2^{\pm}(t))^T = e^{\nu^{\pm}t}v^{\pm}(t)$, $I_{t,\eta}^{\pm} = [V^{\pm}(t) - \vec{\eta}, V^{\pm}(t) + \vec{\eta}]$, and define

$$\delta_0 = \sup\{\eta > 0 : \|DG(v) - DG(V^{\pm}(t))\| \leq \frac{\nu^{\pm}}{2},\ t \in [0,\omega],\ v \in I_{t,\eta}^{\pm}\},$$

$$z_0 = \inf\{\hat{z} > 1 : \|V(t, \pm z) - V^{\pm}(t)\| \leq \frac{\delta_0}{2},\ \forall z \in [\hat{z}, +\infty),\ t \in [0,\omega]\}.$$

It is easy to see that δ_0 and z_0 are well defined due to the fact that $V(t, \pm\infty) = V^{\pm}(t)$ uniformly for $t \in [0, \omega]$.

Let $\zeta(\cdot) \in C^2(\mathbb{R}, \mathbb{R})$ be a function satisfying

$$\zeta(z) = 1 \text{ in } [1, +\infty), \; \zeta(z) = 0 \text{ in } (-\infty, 0],$$

and

$$0 \leq \zeta'(z) \leq 1, \quad |\zeta''(z)| \leq 1, \; \forall z \in \mathbb{R}.$$

Define

$$A(z,t) = \zeta(z)a^+(t) + (1 - \zeta(z))a^-(t),$$

and

$$B(t) = \int_0^t \max\{a_1^+(\tau), a_2^+(\tau), a_1^-(\tau), a_2^-(\tau)\} d\tau.$$

Choose positive constants A, B, C, K such that

$$A = \max_{i,j=1,2}\{\max_{0 \leq t \leq \omega} |DG_i^j(V^+(t))| + \nu^+\},$$

$$B = \max_{i,j=1,2}\{\max_{0 \leq t \leq \omega} |DG_i^j(V^-(t))| + \nu^-\},$$

$$C = \max_{i,j=1,2}\{\max_{0 \leq t \leq \omega}\{|DG_i^j(v)|, v \in [V^-(t) - \vec{1}, V^+(t) + \vec{1}]\}\},$$

$$K \geq 2(A + B + |c| + (d_1 + d_2) + C)/(\min_{t \in [0,\omega], z \in [-z_0, z_0]}\{V_{1z}(t,z), V_{2z}(t,z)\}).$$

Define

$$\tilde{V}(t,z) = V(t, z + K\varepsilon B(t)) + \varepsilon A(t,z).$$

Note that

$$a^\pm(t) = e^{\nu^\pm t} v^\pm(t) = e^{\frac{\mu^\pm t}{2}} s^\pm(t) \leq C^* e^{\frac{\mu^\pm t}{2}},$$

where $C^* = \sup_{t \in [0,\omega]} s^\pm(t)$. It easily follows that $\|a^\pm(t)\|$ and $\|A(t,\cdot)\|$ tend to zero exponentially as $t \to +\infty$, and $B(t)$ is uniformly bounded. Next we show that

$v(t,\cdot,\psi) \le \tilde{V}(t,\cdot)$ in $[0,+\infty) \times \mathbb{R}$ provided that ε is small enough.

Since $\tilde{V}(0,z) = V(0,z) + \varepsilon(\zeta(z)a^+(0) + (1-\zeta(z))a^-(0)) \ge V(0,z) + \varepsilon$, and $v(0,z,\psi) = \psi(z) \le V(0,z) + \varepsilon$, it follows that $v(0,\cdot,\psi) \le \tilde{V}(0,\cdot)$. Letting the spatial argument of V be $z + K\varepsilon B(t)$, then we have

$$\begin{aligned} L(\tilde{V}) :=& \frac{\partial \tilde{V}}{\partial t} - D\frac{\partial^2 \tilde{V}}{\partial z^2} - c\frac{\partial \tilde{V}}{\partial z} - G(\tilde{V}_1, \tilde{V}_2) \\ =& V_t + \varepsilon K B'(t) V_z + \varepsilon A_t - cV_z - \varepsilon c A_z - DV_{zz} - \varepsilon D A_{zz} - G(\tilde{V}_1, \tilde{V}_2) \\ =& \varepsilon K B'(t) V_z + \varepsilon (A_t - cA_z - DA_{zz}) + G(V_1, V_2) - G(\tilde{V}_1, \tilde{V}_2) \\ =& \varepsilon K B'(t) V_z + \varepsilon (A_t - cA_z - DA_{zz}) - \varepsilon \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta. \end{aligned}$$

In order to prove that $\tilde{V}(t,z)$ is an upper solution of system (4.16), we consider three cases: (i) $z \in [z_0,\infty)$, (ii) $z \in (-\infty,-z_0]$, and (iii) $z \in [-z_0, z_0]$.

In the first case, $\zeta(z) = 1$, $A(t,z) = a^+(t) = e^{\nu^+ t} v^+(t)$, and $A_z = A_{zz} = 0$. Then we have

$$\begin{aligned} L(\tilde{V}) \ge& \varepsilon (A_t - \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta \\ =& \varepsilon (\nu^+ e^{\nu^+ t} v^+ + e^{\nu^+ t} DG(V^+(t)) v^+ - \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta) \\ =& \varepsilon (\nu^+ + \int_0^1 (DG(V^+(t)) - DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2)) d\theta) a^+(t) \ge 0 \end{aligned}$$

in $[0,\infty) \times [z_0,\infty)$ provided ε is small enough. Similarly, we can prove $L(\tilde{V}) \ge 0$ in the second case.

In the third case, denote $\bar{a}(t) = (\max\{a_1^-(t), a_1^+(t)\}, \max\{a_2^-(t), a_2^+(t)\})^T \gg 0$. Then we have

$$\begin{aligned} KB'(t)V_z \ge& \vec{K} \max\{a_1^+(t), a_2^+(t), a_1^-(t), a_2^-(t)\} \min_{t\in[0,\omega], z\in[-z_0,z_0]} \{V_{1z}(t,z), V_{2z}(t,z)\} \\ \ge& K\bar{a}(t) \min_{t\in[0,\omega], z\in[-z_0,z_0]} \{V_{1z}(t,z), V_{2z}(t,z)\}, \end{aligned}$$

and

$$
\begin{aligned}
&A_t - cA_z - DA_{zz} - \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta \\
=&\zeta(z)(a^+(t))' + (1 - \zeta(z))(a^-(t))' - c\zeta'(z)(a^+(t) - a^-(t)) \\
&- D\zeta''(z)(a^+(t) - a^-(t)) - \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta \\
=&\zeta(z)(\nu^+ + DG(V^+(t))a^+(t) + (1 - \zeta(z))(\nu^- + DG(V^-(t))a^-(t) \\
&- (c\zeta'(z) + D\zeta''(z))(a^+(t) - a^-(t)) - \int_0^1 DG(V_1 + \varepsilon\theta A_1, V_2 + \varepsilon\theta A_2) A d\theta \\
\geq&(-2A - 2B - 2|c| - 2(d_1 + d_2) - 2C)\bar{a}(t).
\end{aligned}
$$

By the definition of constants A, B, C, K, it then follows that $L(\tilde{V}) \geq 0$ in $[0, \infty) \times [-z_0, z_0]$. Consequently, $\tilde{V}(t, z)$ is an upper solution of system (4.16).

By the comparison principle and $v(0, \cdot, \psi) \leq \tilde{V}(0, \cdot)$, we see that $v(t, \cdot, \psi) \leq \tilde{V}(t, \cdot)$. It then follows from the properties of functions $A(t, z)$ and $B(t)$ that there exist positive constants ε_0, K_0, and ρ_0, such that the lemma holds. □

Lemma 4.3.3. *For any $\psi \in \mathcal{S}$, there exists a positive constant K_1 such that if $\|\psi(\cdot) - V(0, \cdot)\| \leq \varepsilon$ for some $\varepsilon \in (0, \varepsilon_0]$, then*

$$
\|v(t, \cdot, \psi) - V(t, \cdot)\| \leq K_1\varepsilon, \ \forall t \geq 0.
$$

Proof. Letting $\hat{z} = 0$ in Lemma 4.3.2, we see that there exist positive constants K_0, ρ_0 such that

$$
V(t, \cdot - K_0\varepsilon) - K_0\bar{\varepsilon}e^{-\rho_0 t} \leq v(t, \cdot, \psi) \leq V(t, \cdot + K_0\varepsilon) + K_0\bar{\varepsilon}e^{-\rho_0 t}.
$$

It follows that

$$v(t,\cdot,\psi) - V(t,\cdot) \le V(t,\cdot + K_0\varepsilon) - V(t,\cdot) + K_0\vec{\varepsilon}e^{-\rho_0 t},$$

and

$$v(t,\cdot,\psi) - V(t,\cdot) \ge V(t,\cdot - K_0\varepsilon) - V(t,\cdot) - K_0\vec{\varepsilon}e^{-\rho_0 t}.$$

Since $V(t,z)$ is bounded on $\mathbb{R} \times [0,\omega]$, it follows from the local regularity and a priori estimates for parabolic equations that V_z is bounded on $\mathbb{R} \times [0,\omega]$. Then it is easy to see that there exists constant $K_1 > 0$ such that

$$\|v(t,\cdot,\psi) - V(t,\cdot)\| \le K_1\varepsilon, \ \forall t \ge 0.$$

This complete the proof. $\square$

Now we are in a position to prove the main result of this section.

Theorem 4.3.1. *Let $V(t, x-ct)$ be a monotone periodic traveling wave solution of system (4.3) and $\bar{v}(t,x,\psi)$ be the solution of (4.3) with $\bar{v}(0,\cdot,\psi) = \psi(\cdot) \in \mathcal{S}$. Then for any $\psi \in \mathcal{S}$ satisfying (4.15), there exist $s_\psi \in \mathbb{R}$ such that $\lim_{t\to\infty} \|\bar{v}(t,x,\psi) - V(t, x-ct+s_\psi)\| = 0$ uniformly for $x \in \mathbb{R}$. Moreover, any periodic traveling wave solution of (4.3) connecting $V^-(t)$ to $V^+(t)$ is a translation of V.*

Proof. Let $\Omega = [E^1, E^2]_{\mathcal{X}}$, and assume that $\psi \in \mathcal{S}$ satisfies (4.15). Define $\Pi_t(\psi) := v(t,\cdot,\psi), t \ge 0$, that is, $\{\Pi_t\}_{t\ge 0}$ is the periodic semiflow associated with periodic system (4.14). Let $P : \mathcal{S} \to \mathcal{S}$ be the Poincaré map determined by $\{\Pi_t\}_{t\ge 0}$, that is, $P(\psi) := \Pi_\omega(\psi) = v(\omega,\cdot,\psi), \psi \in \mathcal{S}$. Then P is monotone on $\mathcal{S}$ and $P^n(\psi) = \Pi_{n\omega}(\psi)$. By Lemmas 4.3.1 and 4.3.2, there exist a positive integer $\tilde{k}$ and a large number $\tilde{z}$ such that

$$V(t, z - \tilde{z} - K_0\varepsilon_0) - K_0\vec{\varepsilon}_0 e^{-\rho_0 t} \leq \Pi_t(\psi)(z) \leq V(z + \tilde{z} + K_0\varepsilon_0) + K_0\vec{\varepsilon}_0 e^{-\rho_0 t}. \quad (4.17)$$

holds for all $(t, z) \in [\tilde{k}\omega, \infty) \times \mathbb{R}$. Letting $t = n\omega$, we see that $\{P^n(\psi)\}_{n=1}^{\infty}$ is a bounded sequence in $\mathcal{X}$. Note that $V(t, z)$ approaches $V^{\pm}(t)$ as $z \to \pm\infty$ uniformly for $t \in [0, \omega]$. By Ascoli-Arzelà theorem, it then follows that $\gamma^+(\psi) := \{P^n(\psi)\}_{n\geq 0}$ is precompact in $\mathcal{X}$, and hence, the omega limit set $\omega(\psi)$ is nonempty, compact and invariant. Letting $a = \tilde{z} + K_0\varepsilon_0$, and $t = m\omega \to \infty$ in (4.17), we then get $\omega(\psi) \subset I := [V(0, \cdot - a), V(0, \cdot + a)]_{\mathcal{X}}$. Define $h(s) = V(0, \cdot + s), \forall s \in [-a, a]$. Then h is a monotone homeomorphism from $[-a, a]$ onto a subset $\hat{I} \subset I$. By Lemma 4.3.3, each $h(s)$ is a stable fixed point for $P : \mathcal{S} \to \mathcal{S}$. Clearly, each $\phi \in \hat{I}$ satisfies (4.15), and hence, $\gamma^+(\phi)$ is precompact. By Theorem 1.1.2, it suffices to verify condition (3a) to obtain the convergence of $\gamma^+(\psi)$.

Assume that $V(0, \cdot + s_0) < \omega(\phi_0)$ for some $s_0 \in [-a, a)$, and $\phi_0 \in \hat{I}$. Then for each $\phi \in \omega(\phi_0)$, we have $V(0, \cdot + s_0) < \phi(\cdot)$ and $V(0, \cdot + s_0) \not\equiv \phi(\cdot)$ for all $\phi \in \omega(\phi_0)$. By the strong maximum principle, it follows that

$$V(t, z + s_0) \ll \Pi_t(\phi)(z),\ \forall z \in \mathbb{R}, t \geq \omega.$$

Letting $t = \omega$, we get $V(0, z + s_0) \ll P(\phi)(z), \forall z \in \mathbb{R}$. By the invariance of $\omega(\phi_0)$ for P, it follows that

$$V(0, z + s_0) \ll \phi(z),\ \forall \phi \in \omega(\phi_0),\ z \in \mathbb{R}.$$

Since $\lim_{z\to\pm\infty} V_z(0, z) = 0$, we can choose a large positive number $b \in (a, \infty)$ such that $\delta := \sup_{|z|\geq b-a} \|V_z(0, z)\| \leq \frac{1}{4K_0}$. By the compactness of $\omega(\phi_0)$, there exists

$\sigma_0 \in (s_0, a)$ such that

$$V(0, z + \sigma_0) \ll \phi(z), \forall z \in [-b, b], \phi \in \omega(\phi_0).$$

For any fixed $\phi \in \omega(\phi_0)$, there exists a sequence $n_j \to \infty$ such that $P^{n_j}(\phi_0) \to \phi$ as $j \to \infty$. Fix a n_j such that

$$\|P^{n_j}(\phi_0) - \phi\| \leq \delta(\sigma_0 - s_0).$$

Since $V(0, z + \sigma_0) \ll \phi(z)$, $\forall z \in [-b, b]$, and

$$V(0, z + s_0) - V(0, z + \sigma_0) \ll \phi(z) - V(0, z + \sigma_0), \forall z \in \mathbb{R},$$

we have

$$\begin{aligned} P^{n_j}(\phi_0)(z) - V(0, z + \sigma_0) =& P^{n_j}(\phi_0)(z) - \phi(z) + \phi(z) - V(0, z + \sigma_0) \\ \geq& - (\sigma_0 - s_0)\vec{\delta} - \sup_{|z|\geq b} \|V(0, z + s_0) - V(0, z + \sigma_0)\|\vec{e} \\ \geq& - (\sigma_0 - s_0)\vec{\delta} - (\sigma_0 - s_0)\vec{\delta} \\ =& - 2(\sigma_0 - s_0)\vec{\delta}. \end{aligned}$$

By Lemma 4.3.2, it follows that

$$\Pi_t(P^{n_j}(\phi_0)) \geq V(t, \cdot + \sigma_0 - 2K_0(\sigma_0 - s_0)\delta) - 2K_0(\sigma_0 - s_0)\vec{\delta}e^{-\rho_0 t}, \forall t > 0.$$

Letting $t = (n_j - n_k)\omega$ and $j \to \infty$, we get

$$\phi(\cdot) \geq V(0, \cdot + \sigma_0 - 2K_0(\sigma_0 - s_0)\delta) \geq V(0, \cdot + (\sigma_0 + s_0)/2).$$

Let $s_1 = \frac{\sigma_0+s_0}{2}$, then $s_1 \in (s_0, \sigma_0) \subseteq [s_0, \sigma_0]$, and $V(0, \cdot + s_1) \leq_{\mathcal{X}} \phi(\cdot)$. By the arbitrariness of $\phi \in \omega(\phi_0)$, we have $V(0, \cdot + s_1) \leq_{\mathcal{X}} \omega(\phi_0)$.

By Theorem 1.1.2, there exists $s_\psi \in [-a, a]$, such that $\omega(\psi) = h(s_\psi) = V(0, \cdot + s_\psi)$. Thus, $\lim\limits_{n\to\infty} P^n(\psi) = V(0, \cdot + s_\psi)$, and hence $\lim\limits_{n\to\infty} \|\Pi_t(\psi) - V(t, \cdot + s_\psi)\| = 0$. Since

$$\bar{v}(t, x, \psi) = v(t, x - ct, \psi) = \Pi_t(\psi)(x - ct),$$

we have $\lim\limits_{n\to\infty} \|\bar{v}(t, x, \psi) - V(t, x - ct + s_\psi)\| = 0$ uniformly for $x \in \mathbb{R}$.

Let $\tilde{V}(t, x - \tilde{c}t)$ be a time-periodic traveling wave solution of system (4.3) connecting $V^-(t)$ to $V^+(t)$. Clearly, $\tilde{V}(0, \cdot)$ satisfies (4.15) in Lemma 4.3.1. By what we have proved above, there exists $\tilde{s}_\psi \in \mathbb{R}$ such that

$$\lim_{t\to\infty} \|\tilde{V}(t, \cdot - \tilde{c}t) - V(t, \cdot - ct + \tilde{s}_\psi)\| = 0.$$

By change of variable $\tilde{x} = x - ct$, we then have

$$\lim_{t\to\infty} \|\tilde{V}(t, \cdot + (c - \tilde{c})t) - V(t, \cdot + \tilde{s}_\psi)\| = 0.$$

Letting $t = n\omega$, we get $\lim\limits_{n\to\infty} \tilde{V}(0, \cdot + (c - \tilde{c})n\omega) = V(0, \cdot + \tilde{s}_\psi)$. Since $\tilde{V}(0, -\infty) = E^1, \tilde{V}(0, \infty) = E^2$, and $V(0, \cdot)$ is strictly increasing on $\mathbb{R}$, we obtain $\tilde{c} = c$, and hence, $\tilde{V}(t, \cdot) = \Pi_t(\tilde{V}(0, \cdot)) = \Pi_t(V(0, \cdot + s_\psi)) = V(t, \cdot + \tilde{s}_\psi)$ for all $t \geq 0$. $\square$

4.4 Numerical simulations

In this section, we present some numerical simulations to illustrate our analytic results.

By Theorem 4.3.1, we know that the original competition system (4.2) admits a unique bistable traveling wave up to translation, which is globally stable with phase shift. In order to simulate this result, we truncate the infinite domain $\mathbb{R}$ to finite domain $[-L, L]$, where L is sufficiently large. We solve the linear equations and discretize the solutions for bad seasons, while we apply the difference method to discretize the system for good seasons with the Neumann boundary condition. Let $\lambda_1 = 1/10$, $\lambda_2 = 1/12$, $d_1 = 1$, $d_2 = 1/2$, $r_1 = 1/4$, $r_2 = 1/5$, $\alpha = 1/5$, $\beta = 9/10$, $K_1 = 80$, $K_2 = 40$, $\omega = 20$, $\phi = 1/2$. The evolution of two populations and the numerical periodic bistable traveling wave are observed in Figure 4.1 for $L = 200$ with the initial conditions:

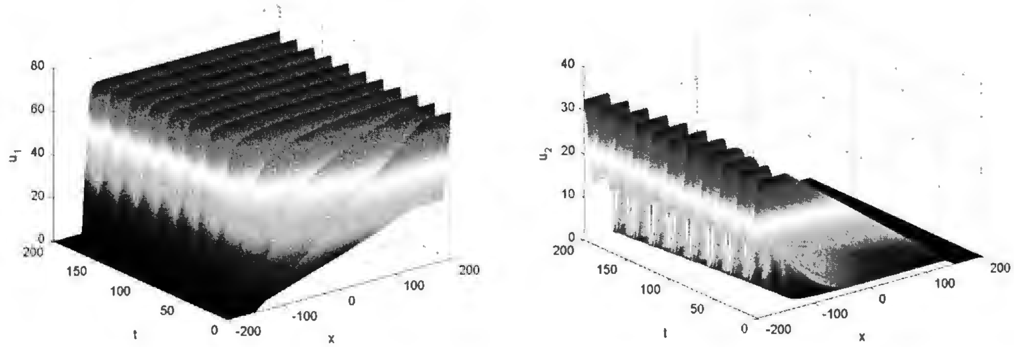
$$u_1(x) = \begin{cases} 1/10, & -200 \leq x \leq -150; \\ 1/10 + (u_1^* - 1/5)(x + 150)/300, & -150 \leq x \leq 150; \\ u_1^* - 1/10, & 150 \leq x \leq 200. \end{cases}$$

$$u_2(x) = \begin{cases} u_2^* - 1/10, & -200 \leq x \leq -150; \\ 1/10 - (u_2^* - 1/5)(x - 150)/300, & -150 \leq x \leq 150; \\ 1/10, & 150 \leq x \leq 200. \end{cases}$$

Here $u_1^* = 67.7073$ and $u_2^* = 31.8550$ are calculated by the the following formulas which are given in the proof of [22, Lemma 2.1]:

$$u_i^* = \frac{K_i(1 - e^{\lambda_i(1-\phi)\omega - r_i\phi\omega})}{1 - e^{-r_i\phi\omega}}.$$

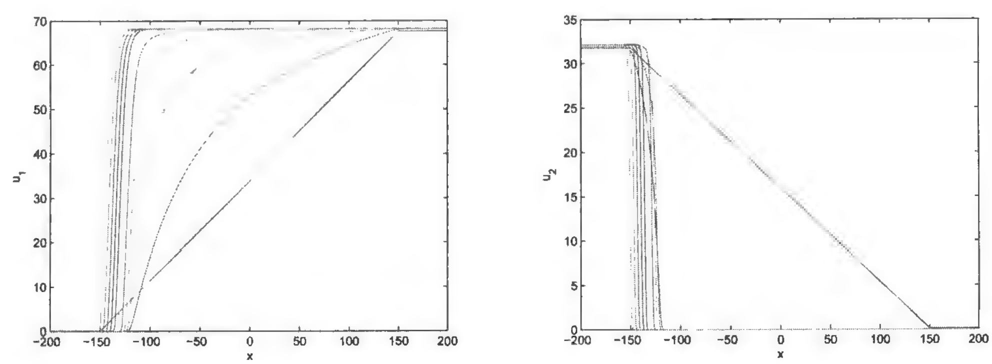
It is well known that the sign of the wave speed of the bistable traveling wave $V(t, x - ct)$ is very important since it tells us which species wins the competition. Mathematically, if $c > 0$ (< 0), then the wave profile move to the right (left) in the x-axis. In order to observe the direction of the traveling wave, that is, the sign of the wave speed c under the given parameters, we plot u_1 and u_2 components with



(a) Population u_1. (b) Population u_2.

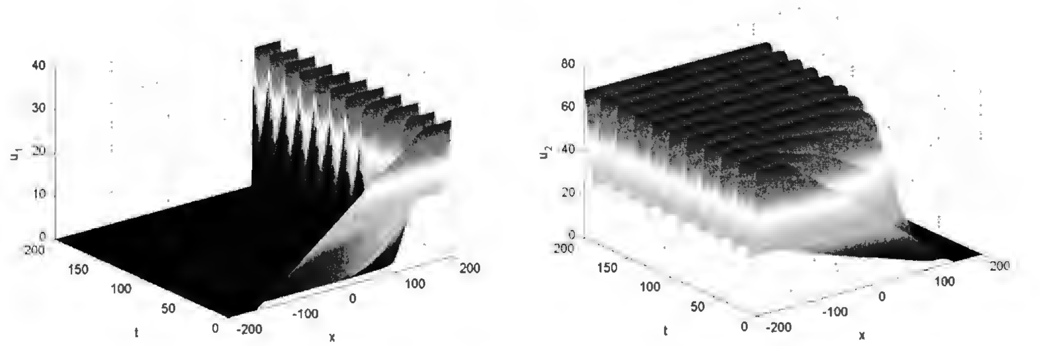
Figure 4.1: The evolution of u_1 and u_2 to a periodic traveling wave.

$t = n\omega$, $n = 0, 1, 2, ..., 10$ in Figure 4.2. We can see, under the given parameters, that the solution rapidly converges to a numerical wave profile, and the sign of the wave speed is negative. In fact, if we exchange the given parameter values corresponding to population u_1 and u_2, respectively, then we observe from Figure 4.3 and 4.4 that the wave speed is positive. Moreover, if we assume the corresponding parameter values are equal, for example, letting $\lambda_1 = \lambda_2 = 1/10$, $d_1 = d_2 = 1$, $r_1 = r_2 = 1/4$, $\alpha = \beta = 9/10$, $K_1 = K_2 = 80$, $\omega = 20$, and $\phi = 1/2$, then we can observe, from Figure 4.5 and 4.6, that the wave speed is 0, that is, the propagation failure occurs.



(a) Population u_1. (b) Population u_2.

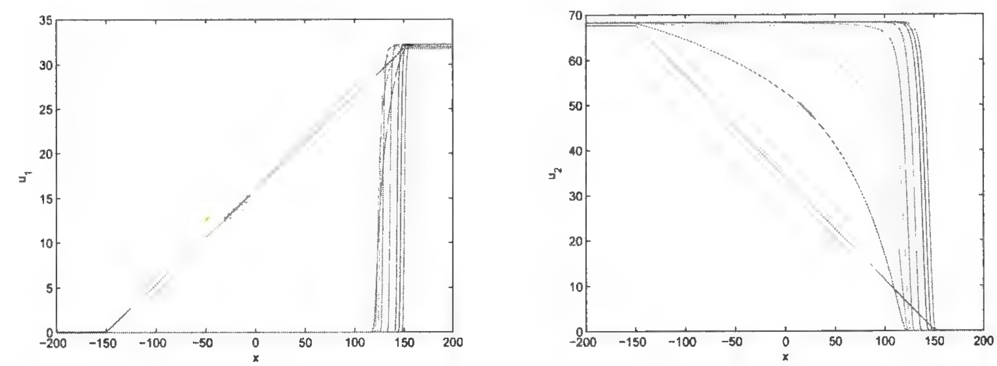
Figure 4.2: u_1 and u_2 at different times $t = n\omega$, $n = 0, 1, 2, ..., 10$.



(a) Population u_1.

(b) Population u_2.

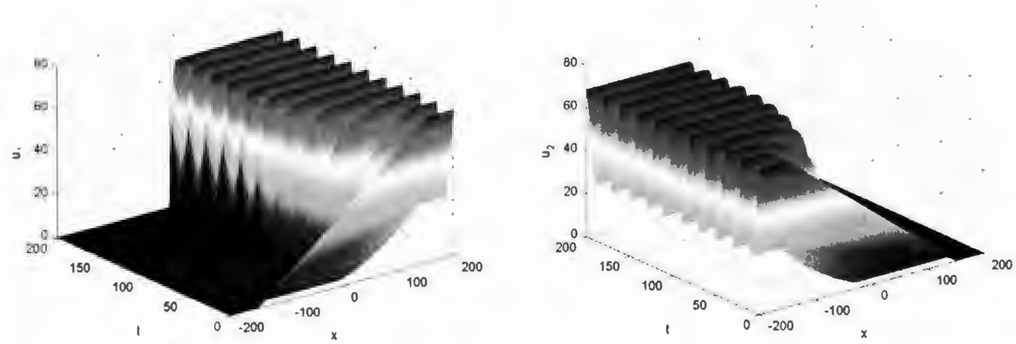
Figure 4.3: The evolution of u_1 and u_2 to a periodic traveling wave.



(a) Population u_1.

(b) Population u_2.

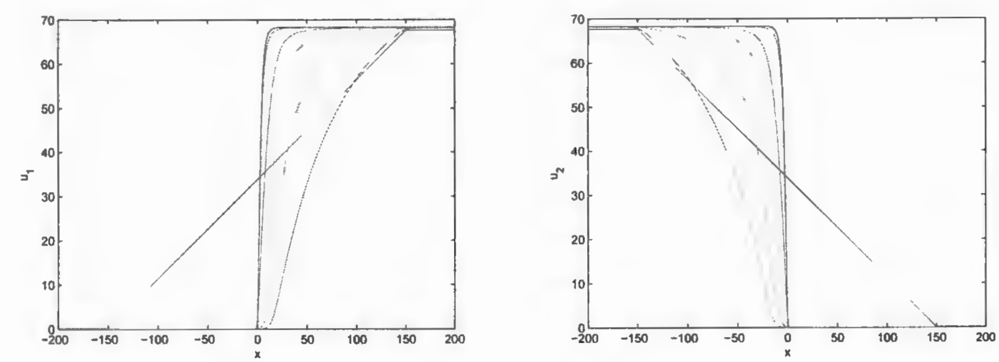
Figure 4.4: u_1 and u_2 at different times $t = n\omega$, $n = 0, 1, 2, ..., 10$.



(a) Population u_1.

(b) Population u_2.

Figure 4.5: The evolution of u_1 and u_2 to a periodic traveling wave.



(a) Population u_1.

(b) Population u_2.

Figure 4.6: u_1 and u_2 at different times $t = n\omega$, $n = 0, 1, 2, ..., 10$.

Chapter 5

A Reaction-Diffusion Lyme Disease Model with Seasonality

5.1 Introduction

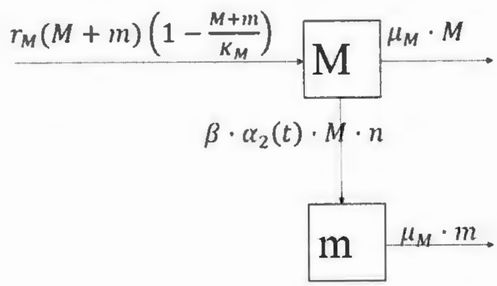
Lyme disease is a commonly reported tick-borne illness, which was named after Lyme, Connecticut, where the first outbreak in humans in North America was recognized in 1975. The disease is caused by the bacterium, *Borrelia burgdorferi*, which is transmitted to humans through the bite of infected ticks. The ticks live for about two years with three feeding stages: larva, nymph and adult. Larval and nymphal ticks primarily feed on mice and adult ticks feed on deer. Larvae that obtain a blood meal drop off their host (mice) and then grow up to the nymphs. These nymphs quest their host (mice) for their blood meal. If they succeed, the nymphs pass the spirochete to susceptible mice and mature to adults. Adults feed almost exclusively on deer and mate there. Female adults eventually drop off the deer and lay their eggs nearby, and die. Larvae hatch and acquire the spirochete when they attack an infected mice for their blood meal. Another tick to mouse to tick infection cycle happens again. For more information about the infection of Lyme disease, we refer to [4, 5, 38, 42, 43, 44] and references therein.

In order to study the effect of vector's stage structure on the transmission dynamics and disease spreading velocity, Caraco et al. [5] proposed a reaction and diffusion model for the Lyme disease in the northeast United States. The model treats population densities at locations $x := (x_1, x_2)$ in a continuous two-dimensional space Ω, and parameters for birth, death, infection, and developmental advance are all positive constants. Recently, Zhao [68] studied the global dynamics of this spatial model for Lyme disease. Note that this model ignores the seasonal pattern in abundances and activities of different stages. As mentioned in [2], seasonal variations in temperature, rainfall and resource availability are ubiquitous and can exert strong pressures on population dynamics. For Lyme disease, the ticks develop slowly or become less active in colder temperatures (see [44]), and the rainfall is also critically important for the development, survival and activities of ticks (see [48]). According to the report from Public Health Agency of Canada on Lyme disease cases in Ontario between 1999-2004 [70], most cases occurred in late spring and summer, when the young ticks are most active and people are outdoors more often. To take seasonal influences into account, we modify Caraco et al.'s model to a reaction and diffusion model in periodic environment. Since the tick development and activities are strongly affected by temperatures [42, 43, 44], we assume that the development rates of ticks and their activity rates (biting rates) are time-dependent. Another assumption is the self-regulation mechanism for the tick population, as discussed in [5]. We assume that the self-regulation process is mainly due to the carrying capacity of hosts and some density-dependent death terms. Let $M(t,x)$ and $m(t,x)$ be the densities of susceptible and pathogen-infected mice; $L(t,x)$ be the density of questing larvae; $V(t,x)$ and $v(t,x)$ be the densities of larvae infesting susceptible and pathogen-infected mice; $N(t,x)$ and $n(t,x)$ be the densities of susceptible and infectious questing nymphs; $A(t,x)$ and $a(t,x)$ be the densities of uninfected and pathogen-infected adult ticks, at time t and location x. From the aforementioned assumptions and the flow digram Figure 5.1. we obtain the following model:

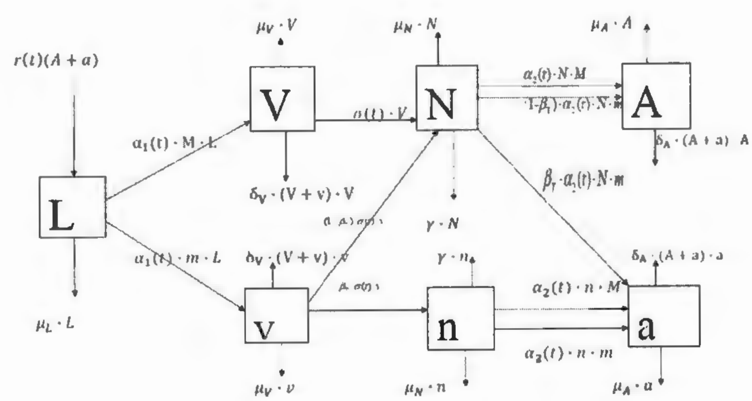
$$
\begin{aligned}
\frac{\partial M}{\partial t} &= D_M \Delta M + r_M(M+m)\left(1 - \frac{M+m}{K_M}\right) - \mu_M M - \alpha_2(t)\beta M n, \\
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta M n - \mu_M m, \\
\frac{\partial L}{\partial t} &= r(t)(A+a) - \mu_L L - \alpha_1(t) L(M+m), \\
\frac{\partial V}{\partial t} &= D_M \Delta V + \alpha_1(t) M L - V(\sigma(t) + \mu_V) - \delta_V(V+v)V, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L - v(\sigma(t) + \mu_V) - \delta_V(V+v)v, \\
\frac{\partial N}{\partial t} &= \sigma(t)[V + (1-\beta_T)v] - N[\gamma + \alpha_2(t)(M+m) + \mu_N], \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t)(M+m) + \mu_N], \\
\frac{\partial A}{\partial t} &= D_H \Delta A + \alpha_2(t) N[M + (1-\beta_T)m] - \mu_A A - \delta_A(A+a)A, \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[(M+m)n + \beta_T m N] - \mu_A a - \delta_A(A+a)a,
\end{aligned} \tag{5.1}
$$

where $\Delta = \frac{\partial^2}{\partial x_1^2} + \frac{\partial^2}{\partial x_2^2}$ is the Laplacian operator on $\mathbb{R}^2$. All constant parameters are positive, and $r(t)$, $\alpha_1(t)$, $\sigma(t)$, and $\alpha_2(t)$ are nonnegative ω-periodic functions. The biological interpretations for the parameters are listed in the Table 5.1. We further assume that $r_M > \mu_M$, $\beta \in (0,1)$, and $\beta_T \in (0,1)$.

Our main purpose in this chapter is to study the global dynamics of system (5.1) in both bounded and unbounded spatial domain. In section 5.2, we obtain a threshold result on the global dynamics of (5.1) in a bounded domain Ω. In section 5.3, we establish the existence of the spreading speed of the disease and its coincidence with the minimal wave speed for periodic traveling waves of system (5.1) when Ω is unbounded. In section 5.4, we present a case study on the transmission of Lyme disease



(a) The schematic diagram for mice.



(b) The schematic diagram for ticks.

Figure 5.1: The schematic diagram for Lyme disease. See Table 5.1 for parameter descriptions.

Table 5.1: The biological interpretations for parameters in Lyme disease model (5.1).

r_M	The individual birth rate of mice.
K_M	Carrying capacity for mice.
μ_M	Mortality rate per mouse.
D_M	Diffusion coefficients for mice.
D_H	Diffusion coefficients for deer.
μ_L	Mortality rate per questing tick larva.
μ_V	Mortality rate per feeding tick larva.
μ_N	Mortality rate per questing tick nymph.
μ_A	Mortality rate per adult tick.
δ_V	Self-regulation coefficient for tick larva.
δ_A	Self-regulation coefficient for adult tick.
β	Susceptibility to infection in mice.
β_T	Susceptibility to infection in ticks.
γ	Biting rate per nymph to humans.
$r(t)$	The individual birth rate of tick at time t.
$\sigma(t)$	The individual development rate of nymph at time t.
$\alpha_1(t)$	The individual biting rate of larva to mice at time t.
$\alpha_2(t)$	The individual biting rate of nymph to mice at time t.

in Port Dove, Ontario. A short discussion section completes the chapter in section 5.5.

5.2 Threshold dynamics in a bounded domain

In this section, we consider system (5.1) in a bounded domain $\Omega \subset \mathbb{R}^2$ with smooth boundary $\partial\Omega$. We assume that all populations remain confined to the domain Ω for all time, and hence, the model system (5.1) is subject to the Neumann boundary conditions:

$$\frac{\partial M}{\partial \nu} = \frac{\partial m}{\partial \nu} = \frac{\partial V}{\partial \nu} = \frac{\partial v}{\partial \nu} = \frac{\partial A}{\partial \nu} = \frac{\partial a}{\partial \nu} = 0,$$

where $\frac{\partial}{\partial \nu}$ represents the differentiation along the outward normal ν to $\partial\Omega$.

For the convenience of mathematical analysis, we make a change of variables $\mathcal{M} =$

$\mathcal{M} + m$, $\mathcal{V} = V + v$, $\mathcal{N} = N + n$, $\mathcal{A} = A + a$ for system (5.1). It then follows that system (5.1) is equivalent to the following one:

$$
\begin{aligned}
\frac{\partial \mathcal{M}}{\partial t} &= D_M \Delta \mathcal{M} + r_M \mathcal{M}\left(1 - \frac{\mathcal{M}}{K_M}\right) - \mu_M \mathcal{M}, \\
\frac{\partial L}{\partial t} &= r(t)\mathcal{A} - \mu_L L - \alpha_1(t) L \mathcal{M}, \\
\frac{\partial \mathcal{V}}{\partial t} &= D_M \Delta \mathcal{V} + \alpha_1(t)\mathcal{M}L - \mathcal{V}(\sigma(t) + \mu_V) - \delta_V \mathcal{V}^2, \\
\frac{\partial \mathcal{N}}{\partial t} &= \sigma(t)\mathcal{V} - \mathcal{N}[\gamma + \alpha_2(t)\mathcal{M} + \mu_N], \\
\frac{\partial \mathcal{A}}{\partial t} &= D_H \Delta \mathcal{A} + \alpha_2(t)\mathcal{N}\mathcal{M} - \mu_A \mathcal{A} - \delta_A \mathcal{A}^2, \\
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta(\mathcal{M} - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L - v(\sigma(t) + \mu_V) - \delta_V \mathcal{V} v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t)\mathcal{M} + \mu_N], \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[\mathcal{M}n + \beta_T m(\mathcal{N} - n)] - \mu_A a - \delta_A \mathcal{A} a,
\end{aligned}
\tag{5.2}
$$

Note that the first five equations in (5.2) do not depend on the others. In addition, by the condition $r_M > \mu_M$ and a standard convergence result on the logistic type reaction-diffusion equation (see, e.g., Theorem 3.1.5 and the proof of Theorem 3.1.6 in [67]), it follows that for any $\mathcal{M}(0, \cdot) \in C(\bar{\Omega}, \mathbb{R}^2_+)\backslash\{0\}$, we have

$$\lim_{t\to\infty} \mathcal{M}(t, x) = K_M\left(1 - \frac{\mu_M}{r_M}\right) := Q$$

uniformly for $x = (x_1, x_2) \in \bar{\Omega}$. Thus, we first analyze the global dynamics of the following limiting system:

$$
\begin{aligned}
\frac{\partial L}{\partial t} &= r(t)\mathcal{A} - L[\mu_L + \alpha_1(t)Q],\\
\frac{\partial \mathcal{V}}{\partial t} &= D_M\Delta\mathcal{V} + \alpha_1(t)QL - \mathcal{V}(\sigma(t) + \mu_V) - \delta_V\mathcal{V}^2,\\
\frac{\partial \mathcal{N}}{\partial t} &= \sigma(t)\mathcal{V} - \mathcal{N}[\gamma + \alpha_2(t)Q + \mu_N],\\
\frac{\partial \mathcal{A}}{\partial t} &= D_H\Delta\mathcal{A} + \alpha_2(t)\mathcal{N}Q - \mu_A\mathcal{A} - \delta_A\mathcal{A}^2.
\end{aligned} \tag{5.3}
$$

Let $X = C(\bar{\Omega}, \mathbb{R}^4)$, $X^+ = C(\bar{\Omega}, \mathbb{R}^4_+)$, and $\Gamma(t, x, y)$ be the Green function associated with the Laplacian operator Δ and the Neumann boundary condition, and define

$$
\begin{aligned}
[T_1(t,s)\phi_1](x) &= e^{-\int_s^t(\mu_L+\alpha_1(\tau)Q)d\tau}\phi_1(x),\\
[T_2(t,s)\phi_2](x) &= e^{-\int_s^t(\sigma(\tau)+\mu_V)d\tau}\int_\Omega \Gamma(D_M(t-s),x,y)\phi_2(y)dy,\\
[T_3(t,s)\phi_3](x) &= e^{-\int_s^t(\gamma+\alpha_2(\tau)Q+\mu_N)d\tau}\phi_3(x),\\
[T_4(t,s)\phi_4](x) &= e^{-\mu_A(t-s)}\int_\Omega \Gamma(D_H(t-s),x,y)\phi_4(y)dy.
\end{aligned}
$$

Then system (5.3) can be written as the following integral equations:

$$
\begin{aligned}
L(t,x) &= T_1(t,0)L(0,x) + \int_0^t T_1(t,s)r(s)\mathcal{A}(s,x)ds,\\
\mathcal{V}(t,x) &= T_2(t,0)\mathcal{V}(0,x) + \int_0^t T_2(t,s)(\alpha_1(s)QL(s,x) - \delta_V\mathcal{V}^2(s,x))ds,\\
\mathcal{N}(t,x) &= T_3(t,0)\mathcal{N}(0,x) + \int_0^t T_3(t,s)\sigma(s)\mathcal{V}(s,x)ds,\\
\mathcal{A}(t,x) &= T_4(t,0)\mathcal{A}(0,x) + \int_0^t T_4(t,s)(\alpha_2(s)Q\mathcal{N}(s,x) - \delta_A\mathcal{A}^2(s,x))ds.
\end{aligned} \tag{5.4}
$$

By the theory of abstract semilinear integral equations in [41], it follows that for any

$\phi \in X^+$, system (5.4) admits a unique nonnegative and non-continuable solution

$$u(t,x,\phi) := (L(t,x,\phi), \mathcal{V}(t,x,\phi), \mathcal{N}(t,x,\phi), \mathcal{A}(t,x,\phi))$$

on $[0,\sigma_\phi)$ with $u(0,\cdot,\phi) = \phi$. Moreover, it follows from [41, Proposition 1 and Remark 1.4] that system (5.4) admits the comparison principle.

Note that the spatially homogeneous system of (5.3) is the following periodic system of ordinary differential equations:

$$\begin{aligned}
\frac{dL}{dt} &= r(t)\mathcal{A} - L[\mu_L + \alpha_1(t)Q], \\
\frac{d\mathcal{V}}{dt} &= \alpha_1(t)QL - \mathcal{V}(\sigma(t) + \mu_V) - \delta_V\mathcal{V}^2, \\
\frac{d\mathcal{N}}{dt} &= \sigma(t)\mathcal{V} - \mathcal{N}[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{d\mathcal{A}}{dt} &= \alpha_2(t)\mathcal{N}Q - \mu_A\mathcal{A} - \delta_A\mathcal{A}^2,
\end{aligned} \tag{5.5}$$

and every nonnegative solution $(L(t), \mathcal{V}(t), \mathcal{N}(t), \mathcal{A}(t))$ of (5.5) satisfies

$$\frac{d}{dt}(L(t)+\mathcal{V}(t)+\mathcal{N}(t)+\mathcal{A}(t)) = (r(t)-\mu_A-\delta_A\mathcal{A})\mathcal{A}-\mu_L L-\mu_V\mathcal{V}-\delta_V\mathcal{V}^2-\mathcal{N}(\gamma+\mu_N) < 0$$

provided $\mathcal{A} > (\max_{0\le t\le\omega} r(t) - \mu_A)/\delta_A$. It then follows that solutions of (5.5) are ultimately bounded in $\mathbb{R}^4_+$ and exist for all $t \in [0,\infty)$.

Linearing system (5.5) at $(0,0,0,0)$, we get the following linear cooperative system:

$$\begin{aligned}
\frac{dL}{dt} &= r(t)\mathcal{A} - L[\mu_L + \alpha_1(t)Q], \\
\frac{d\mathcal{V}}{dt} &= \alpha_1(t)QL - \mathcal{V}(\sigma(t) + \mu_V), \\
\frac{d\mathcal{N}}{dt} &= \sigma(t)\mathcal{V} - \mathcal{N}[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{d\mathcal{A}}{dt} &= \alpha_2(t)\mathcal{N}Q - \mu_A\mathcal{A}.
\end{aligned} \tag{5.6}$$

Let r_1 be the spectral radius of the Poincaé map associated with system (5.6). Then it is easy to see r_1 is the principal Floquet multiplier of system (5.6). Further we have the following result.

Lemma 5.2.1. *The following statements are valid:*

(i) If $r_1 \leq 1$, then (0,0,0,0) is globally asymptotically stable for (5.5) *in* $\mathbb{R}^4_+$.

(ii) If $r_1 > 1$, then (5.5) *admits a unique positive ω-periodic solution $u^*(t) := (L^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t))$, which is globally asymptotically stable for* (5.5) *in* $\mathbb{R}^4_+ \backslash \{0\}$.

Proof. Define $f = (f_1, f_2, f_3, f_4) : \mathbb{R}^4 \to \mathbb{R}^4$ by

$$
\begin{aligned}
f_1(x_1, x_2, x_3, x_4) &= r(t)x_4 - x_1[\mu_L + \alpha_1(t)Q], \\
f_2(x_1, x_2, x_3, x_4) &= \alpha_1(t)Qx_1 - x_2(\sigma(t) + \mu_V) - \delta_V x_2^2, \\
f_3(x_1, x_2, x_3, x_4) &= \sigma(t)x_2 - x_3[\gamma + \alpha_2(t)Q + \mu_N], \\
f_4(x_1, x_2, x_3, x_4) &= \alpha_2(t)x_3Q - \mu_A x_4 - \delta_A x_4^2.
\end{aligned}
$$

It is easy to verify that $f_i \geq 0$ for any $x = (x_1, x_2, x_3, x_4) \in \mathbb{R}^4_+$ with $x_i = 0$, and the Jacobian matrix of $f(x_1, x_2, x_3, x_4)$ is cooperative for any $x \in \mathbb{R}^4_+$. Thus, the solution semiflow $\{\Pi_t\}_{t\geq 0}$ determined by (5.5) is monotone in the sense that $\Pi_t(x) \geq \Pi_t(y)$ provided $x \geq y$ in $\mathbb{R}^4_+$. Next, we show that Π_t is strongly monotone for all $t \geq 3\omega$, that is, $\Pi_t(x) \gg \Pi_t(y)$ whenever $t \geq 3\omega$ and $x > y$. Let $x(t) := (x_1(t), x_2(t), x_3(t), x_4(t)) = \Pi_t(x_0)$, $y(t) := (y_1(t), y_2(t), y_3(t), y_4(t)) = \Pi_t(y_0)$, and $z(t) := (z_1(t), z_2(t), z_3(t), z_4(t)) = x(t) - y(t)$. Then $z(t)$ satisfies the following equations:

$$
\begin{aligned}
\frac{dz_1}{dt} &= r(t)z_4 - z_1[\mu_L + \alpha_1(t)Q], \\
\frac{dz_2}{dt} &= \alpha_1(t)Qz_1 - z_2(\sigma(t) + \mu_V + \delta_V(x_2(t) + y_2(t))), \\
\frac{dz_3}{dt} &= \sigma(t)z_2 - z_3[\gamma + \alpha_2(t)Q + \mu_N], \\
\frac{dz_4}{dt} &= \alpha_2(t)Qz_3 - z_4(\mu_A + \delta_A(x_4(t) + y_4(t))).
\end{aligned} \tag{5.7}
$$

Now it suffices to prove $z(t) \gg 0$, $\forall t \geq 3\omega$, whenever $z(0) = x_0 - y_0 > 0$. Denote $\frac{dz}{dt} = A(t)z$, where $A(t) := (a_{ij}(t)), 1 \leq i, j \leq 4$, is the coefficient matrix of the right hand side of (5.7). Since $a_{ij}(t) \geq 0$. $i \neq j$, we have $\frac{dz_i}{dt} \geq a_{ii}(t)z_i, 1 \leq i \leq 4$. Using this fact, we can see that $z_i(t)$ remains positive for all $t \geq t^*$ if it becomes so at $t = t^*$. Then it suffices to show that at least one of the component becomes strictly positive, and that once this happens, all other components will eventually becomes strictly positive. Note that $z(0) > 0$ implies that at least one of the component of $z(0)$ is strictly positive. Without loss of generality, we suppose $z_1(0) > 0$. From above analysis, we know that $z_1(t) > 0$ for all $t \geq 0$. Now we claim that there exists $t_1 \in [0, \omega]$ such that $z_2(t_1) > 0$. Otherwise, we have $z_2(t) \equiv 0, \forall t \in [0, \omega]$. From z_2 equation in (5.7), we further derive that $\alpha_1(t)Qz_1 \equiv 0, \forall t \in [0, \omega]$. Since $\alpha_1(t)$ is periodic and not identically zero, there must be some $\bar{t} \in [0, \omega]$ such that $z_1(\bar{t}) = 0$, which is a contradiction. Similarly, by z_3 equation in (5.7) and the fact that $\sigma(t)$ is periodic and not identically zero, we can prove there exists $t_2 \in [t_1, t_1 + \omega]$ such that $z_3(t_2) > 0$. Furthermore, by the z_4 equation in (5.7) and the properties of $\alpha_2(t)$, we see that there exists $t_3 \in [t_2, t_2 + \omega]$ such that $z_4(t_3) > 0$. Since $t_3 \in [0, 3\omega]$, we have proved that Π_t is strongly monotone when $t \geq 3\omega$. Clearly, other cases can be proved in a similar way. Therefore, $\Pi_{3\omega}$ is strongly monotone. It is easy to see that $f(x_1, x_2, x_3, x_4)$ is strictly subhomogeneous in the sense that $f(sx_1, sx_2, sx_3, sx_4) > sf(x_1, x_2, x_3, x_4)$ for all $s \in (0,1)$ and $(x_1, x_2, x_3, x_4) \in \text{int}(\mathbb{R}^4_+)$. By Theorem 1.1.3, as applied to $\Pi_{3\omega}$, it follows that statement (i) is valid, and that in the case of $r_1 > 1$, there exists a unique 3ω-periodic solution $u^*(t) := (L^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t))$, which is globally asymptotically stable for all solutions of (5.5) with initial values in $\mathbb{R}^4_+ \backslash \{0\}$. Clearly, $u^*(0)$ is a unique fixed point of $\Pi_{3\omega}$. By the properties of the periodic semiflow, we further get

$$\Pi_{3\omega}(\Pi_\omega(u^*(0))) = \Pi_\omega(\Pi_{3\omega}(u^*(0))) = \Pi_\omega(u^*(0)),$$

which implies that $\Pi_\omega(u^*(0))$ is also a fixed point of $\Pi_{3\omega}$. By the uniqueness of the fixed point of $\Pi_{3\omega}$, it follows that $\Pi_\omega(u^*(0)) = u^*(0)$. Thus, $u^*(t)$ is a ω-periodic solution of (5.5) and statement (ii) is valid. $\square$

By Lemma 5.2.1 and the comparison principle, we know that solutions of system (5.3) are ultimately bounded in X^+, and hence, $\sigma_\phi = \infty$ for all $\phi \in X^+$. Let $\Phi_t : X^+ \to X^+, t \geq 0$, be the solution semiflow associated with (5.3), that is, $\Phi_t(\phi) = u(t, \cdot, \phi), \forall \phi \in X^+$. Define a linear operator $\mathcal{L}(t)\phi = (T_1(t,0)\phi_1, 0, T_3(t,0)\phi_3, 0)$, and

$$\mathcal{S}(t)\phi = \left(\int_0^t T_1(t,s) r(s) \mathcal{A}(s, \cdot, \phi) ds, \mathcal{V}(t, \cdot, \phi), \int_0^t T_3(t,s) \sigma(s) \mathcal{V}(s, \cdot, \phi) ds, \mathcal{A}(t, \cdot, \phi) \right).$$

Then $\Phi_t(\phi) = \mathcal{L}(t)\phi + \mathcal{S}(t)\phi$. By the same decomposition argument as in the proof of [68, Lemma 3.1], it follows that Φ_t is an α-contraction operator for any given $t > 0$. Combining the arguments in Lemma 5.2.1 and the positivity result for reaction-diffusion equations, we can further show that Φ_t is strongly positive for all $t \geq 3\omega$, that is, $\Phi_t(\phi) \gg 0$ for any $t \geq 3\omega$ and initial data $\phi > 0$ in X^+. Note that solutions of system (5.5) are also solutions of the reaction-diffusion system (5.3) subject to Neumann boundary conditions. Thus, Lemma 5.2.1 and the standard comparison principle arguments give rise to the following result.

Theorem 5.2.1. *For any given $\phi \in X^+$, let $u(t, \cdot, \phi)$ be the solution of (5.3) with $u(0, \cdot, \phi) = \phi$. Then the following two statement are valid:*

(i) If $r_1 \le 1$, then $(0, 0, 0, 0)$ is globally asymptotically stable for (5.3) in X^+.

(ii) If $r_1 > 1$, then $u^*(t)$ is globally asymptotically stable for (5.3) in $X^+ \backslash \{0\}$.

Next we consider the global dynamics of the following limiting system:

$$\begin{aligned}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L^*(t) - v(\sigma(t) + \mu_V) - \delta_V \mathcal{V}^*(t) v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) Q + \mu_N], \\
\frac{\partial a}{\partial t} &= D_H \Delta a + \alpha_2(t)[Qn + \beta_T m(\mathcal{N}^*(t) - n)] - \mu_A a - \delta_A \mathcal{A}^*(t) a.
\end{aligned} \tag{5.8}$$

Let $Y = C(\bar{\Omega}, [0, Q] \times \mathbb{R}_+^2) \times C(\bar{\Omega}, \mathbb{R}_+)$. It then follows that any $\phi \in Y$, system (5.8) admits a unique solution $w(t, x, \phi) := (m(t, x, \phi), v(t, x, \phi), n(t, x, \phi), a(t, x, \phi))$ on $[0, \infty)$ with $w(0, \cdot, \phi) = \phi$, and $w(t, x, \phi) \in Y, \forall t > 0$. Moreover, by the ultimate boundness of $\mathcal{V}, \mathcal{N}, \mathcal{A}$, we see that $w(t, x, \phi)$ is also ultimately bounded.

Note that the spatially homogeneous system associated with (5.8) is the following system:

$$\begin{aligned}
\frac{dm}{dt} &= \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{dv}{dt} &= \alpha_1(t) m L^*(t) - v(\sigma(t) + \mu_V) - \delta_V \mathcal{V}^*(t) v, \\
\frac{dn}{dt} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) Q + \mu_N], \\
\frac{da}{dt} &= \alpha_2(t)[Qn + \beta_T m(\mathcal{N}^*(t) - n)] - \mu_A a - \delta_A \mathcal{A}^*(t) a,
\end{aligned} \tag{5.9}$$

and $(0, 0, 0, 0)$ is an ω-periodic solution of (5.9). Linearizing system (5.9) at $(0, 0, 0, 0)$, we get the following linear system

$$\begin{aligned}
\frac{dm}{dt} &= \alpha_2(t)\beta Q n - \mu_M m, \\
\frac{dv}{dt} &= \alpha_1(t) m L^*(t) - v(\sigma(t) + \mu_V) - \delta_V \mathcal{V}^*(t) v, \\
\frac{dn}{dt} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) Q + \mu_N], \\
\frac{da}{dt} &= \alpha_2(t) Q n + \beta_T \alpha_2(t) \mathcal{N}^*(t) m - \mu_A a - \delta_A \mathcal{A}^*(t) a.
\end{aligned} \tag{5.10}$$

In order to introduce the basic reproduction ratio for system (5.9), we follow the procedure in [59]. We rewrite system (5.10) as $\frac{du}{dt} = (F(t) - V(t))u$, where

$$F(t) = \begin{pmatrix} 0 & 0 & \alpha_2(t)\beta Q & 0 \\ \alpha_1(t) L^*(t) & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ \beta_T \alpha_2(t) \mathcal{N}^*(t) & 0 & 0 & 0 \end{pmatrix},$$

$$V(t) = \begin{pmatrix} \mu_M & 0 & 0 & 0 \\ 0 & \sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t) & 0 & 0 \\ 0 & -\beta_T \sigma(t) & \gamma + \alpha_2(t) Q + \mu_N & 0 \\ 0 & 0 & -\alpha_2(t) Q & \mu_A + \delta_A \mathcal{A}^*(t) \end{pmatrix}.$$

Let $Y(t,s), t \geq s$, be the evolution operator of the linear system $\frac{du}{dt} = -V(t)u$. That is, for each $s \in \mathbb{R}$, the matrix $Y(t,s)$ satisfies

$$\frac{d}{dt} Y(t,s) = -V(t) Y(t,s), \ \forall t \geq s, \ Y(s,s) = I,$$

where I is the 4×4 identity matrix.

Let C_ω be the Banach space of all ω-periodic functions from $\mathbb{R}$ to $\mathbb{R}^2$, equipped with the maximum norm. Suppose $\phi(s) \in C_\omega$ is the initial distribution of infectious individuals in this periodic environment, then $F(s)\phi(s)$ is the rate of new infections produced by the infected individuals who were introduced at time s, and $Y(t,s)F(s)\phi(s)$ represents the distribution of those infected individuals who were newly infected at time s and remain in the infected compartments at time t for $t \geq s$. Hence,

$$\int_{-\infty}^{t} Y(t,s)F(s)\phi(s)ds = \int_{0}^{\infty} Y(t,t-\tau)F(t-\tau)\phi(t-\tau)d\tau$$

gives the distribution of accumulative new infection at time t produced by all those infected individuals $\phi(s)$ introduced at previous time. Define a linear operator $L : C_\omega \to C_\omega$ by

$$(L\phi)(t) = \int_{0}^{\infty} Y(t,t-\tau)F(t-\tau)\phi(t-\tau)d\tau, \forall t \in \mathbb{R}, \phi \in C_\omega.$$

According to [3, 59], we define the basic reproduction ratio to be $R_0 := r(L)$, where $r(L)$ is the spectral radius of L.

Let r_2 be the principle Floquet multiplier of the linear system (5.10). Then Theorem 1.3.1 implies that $R_0 - 1$ has the same sign as $r_2 - 1$. Thus, $(0,0,0,0)$ is asymptotically stable if $R_0 < 1$, and unstable if $R_0 > 1$.

Since the first three equations in system (5.9) do not depend on the fourth one, we consider the following subsystem of system (5.9):

$$\begin{aligned}
\frac{dm}{dt} &= \alpha_2(t)\beta(Q-m)n - \mu_M m,\\
\frac{dv}{dt} &= \alpha_1(t)mL^*(t) - v(\sigma(t)+\mu_V) - \delta_V \mathcal{V}^*(t)v,\\
\frac{dn}{dt} &= \beta_T\sigma(t)v - n[\gamma + \alpha_2(t)Q + \mu_N].
\end{aligned} \tag{5.11}$$

Let r_3 be the principle Floquet multiplier of the following periodic linear system:

$$\begin{aligned}\frac{dm}{dt} &= \alpha_2(t)\beta Qn - \mu_M m,\\ \frac{dv}{dt} &= \alpha_1(t)mL^*(t) - v(\sigma(t)+\mu_V) - \delta_V\mathcal{V}^*(t)v,\\ \frac{dn}{dt} &= \beta_T\sigma(t)v - n[\gamma+\alpha_2(t)Q+\mu_N].\end{aligned} \tag{5.12}$$

Comparing system (5.10) and (5.12), it is easy to see that $r_3 - 1$ has the same sign as $r_2 - 1$. Then we have the following threshold result for system (5.9) in terms of R_0.

Lemma 5.2.2. *The following statements are valid:*

(i) *If $R_0 \le 1$, then (0,0,0,0) is globally asymptotically stable for* (5.9) *in* $[0,Q]\times\mathbb{R}^3_+$.

(ii) *If $R_0 > 1$, then* (5.9) *admits a unique positive ω-periodic solution $w^*(t) := (m^*(t), v^*(t), n^*(t), a^*(t))$, which is globally asymptotically stable for* (5.9) *in* $([0,Q]\times\mathbb{R}^2_+\backslash\{0\})\times\mathbb{R}_+$.

Proof. We first show that the following threshold result holds for system (5.11):

(a) If $r_3 \le 1$, then (0,0,0) is globally asymptotically stable for (5.11) in $[0,Q]\times\mathbb{R}^2_+$.

(b) If $r_3 > 1$, then (5.11) has a positive ω-periodic solution $(m^*(t), v^*(t), n^*(t))$, which is globally asymptotically stable for (5.11) in $([0,Q]\times\mathbb{R}^2_+)\backslash\{0\}$.

Let $\bar{w}(t,\bar{w}_0)$ be the nonnegative solution of system (5.11) with initial data $\bar{w}_0 \in [0,Q]\times\mathbb{R}^2_+$. Denote $X(t) = \frac{\partial\bar{w}}{\partial\bar{w}_0}(t,\bar{w}_0)$. Then $X(t) = (x_{ij}(t))_{3\times 3}$ satisfies

$$X'(t) = A(t)X(t),\ X(0) = I,$$

where $A(t) = (a_{ij}(t))_{3\times 3}$ is the Jacobian matrix of the right hand side of system (5.11) evaluated at $(m,v,n) = \bar{w}(t,\bar{w}_0)$. Since $a_{ij}(t) \ge 0, i \ne j, \forall t \ge 0$, we have

$x'_{ij}(t) \geq a_{ii}(t)x_{ij}(t), \forall t \geq 0, 1 \leq i, j \leq 3$. It then follows that $x_{ij}(t) > 0$ for all $t \geq t^*$ provided $x_{ij}(t^*) > 0$ for some $t^* \geq 0$. Since $x_{ii}(0) = 1$, we have $x_{ii}(t) > 0$ for all $t \geq 0, 1 \leq i \leq 3$. We further prove that $x_{ij}(t) > 0$ for all $t \geq 2\omega$. Note that $x_{ij}(t), i \neq j$, satisfy the following equations:

$$
\begin{aligned}
x'_{12}(t) &= -(\alpha_2(t)\beta n(t) + \mu_M)x_{12}(t) + \alpha_2(t)\beta(Q - m(t))x_{32}(t), \\
x'_{13}(t) &= -(\alpha_2(t)\beta n(t) + \mu_M)x_{13}(t) + \alpha_2(t)\beta(Q - m(t))x_{33}(t), \\
x'_{21}(t) &= \alpha_1(t)L^*(t)x_{11}(t) - (\sigma(t) + \mu_V + \mathcal{V}^*(t)\delta_V)x_{21}(t), \\
x'_{23}(t) &= \alpha_1(t)L^*(t)x_{13}(t) - (\sigma(t) + \mu_V + \mathcal{V}^*(t)\delta_V)x_{23}(t), \\
x'_{31}(t) &= \beta_T\sigma(t)x_{21}(t) + (\gamma + \alpha_2(t)Q + \mu_N)x_{31}(t), \\
x'_{32}(t) &= \beta_T\sigma(t)x_{22}(t) + (\gamma + \alpha_2(t)Q + \mu_N)x_{32}(t).
\end{aligned}
$$

Since $x_{ii}(t) > 0, \forall t \geq 0, 1 \leq i \leq 3$, and $\alpha_1(t), \alpha_2(t), \sigma(t)$ are periodic but not identically zero, it follows from a contradiction argument that there exists $t_1 \in [0, \omega]$ such that $x_{13}(t), x_{21}(t), x_{32}(t) > 0$ for all $t \geq t_1$. Then we can prove that there exists $t_2 \in [t_1, t_1 + \omega]$ such that $x_{12}(t), x_{23}(t), x_{31}(t) > 0$ for all $t \geq t_2$. Since $t_2 \in [0, 2\omega]$, we have $X(t) \gg 0, \forall t \geq 2\omega$. Then for any $\bar{w}_1, \bar{w}_2 \in \mathbb{R}^3_+$ satisfying $\bar{w}_2 > \bar{w}_1$, we have

$$
\bar{w}(t, \bar{w}_2) - \bar{w}(t, \bar{w}_1) = \int_0^1 \frac{\partial \bar{w}}{\partial \bar{w}_0}(t, \bar{w}_1 + r(\bar{w}_2 - \bar{w}_1))(\bar{w}_2 - \bar{w}_1)dr \gg 0
$$

provided $t \geq 2\omega$. This implies that $\bar{w}_t(\bar{w}_2) \gg \bar{w}_t(\bar{w}_1)$ for all $t \geq 2\omega$. In particular, we have $\bar{w}_{2\omega}(\cdot)$ is strongly monotone. By the same argument as in the proof of Lemma 5.2.1, we see that statements (a) and (b) hold.

By the theory of chain transitive sets (see [20] or [67, Section 1.2]) and the similar arguments as those in the proof of Theorem 5.2.3, it follows that $\lim_{t\to\infty} a(t) = 0$ in the case where $r_3 \leq 1$, and $\lim_{t\to\infty}(a(t) - a^*(t)) = 0$ in the case where $r_3 > 1$, where

$a^*(t)$ is the unique positive ω-periodic solution of the following limiting equation

$$\frac{da}{dt} = \alpha_2(t)[Qn^*(t) + \beta_T m^*(t)(\mathcal{N}^*(t) - n^*(t))] - (\mu_A + \delta_A \mathcal{A}^*(t))a.$$

Since $r_3 - 1$ has the same sign as $R_0 - 1$, we then complete the proof. $\square$

The following result shows that R_0 is also the threshold value for the global dynamics of system (5.8).

Theorem 5.2.2. *For any given $\phi \in Y$, let $w(t, \cdot, \phi)$ be the solution of (5.8) with $w(0, \cdot, \phi) = \phi$. Then the following two statement are valid:*

(i) If $R_0 \leq 1$, then $(0, 0, 0, 0)$ is globally asymptotically stable for (5.8) in Y.

(ii) If $R_0 > 1$, then $w^*(t)$ is globally asymptotically stable for (5.8) in $(C(\bar{\Omega}, [0, Q) \times \mathbb{R}_+^2) \backslash \{0\}) \times C(\bar{\Omega}, \mathbb{R}_+)$.

Proof. Since the first three equations in (5.8) do not depend on the forth one, it suffices to prove that the threshold result is valid for the following subsystem:

$$\begin{aligned}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta(Q - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L^*(t) - v(\sigma(t) + \mu_V) - \delta_V \mathcal{V}^*(t) v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) Q + \mu_N].
\end{aligned} \tag{5.13}$$

Let $\hat{w}(t, \cdot, \hat{\phi})$ be the unique solution of (5.13) with the initial data $\hat{\phi} \in C(\bar{\Omega}, [0, Q] \times \mathbb{R}_+^2) \backslash \{0\}$. By the positivity result for reaction-diffusion equations, it follows that $\hat{w}(t, \cdot, \hat{\phi}) \gg 0, \forall t \geq 2\omega$. Note that solutions of system (5.11) are also solutions of the reaction-diffusion system (5.13) subject to Neumann boundary conditions. Thus, Lemma 5.2.2, together with the standard comparison argument, implies that the threshold result is valid for system (5.13). $\square$

In the rest of this section, we use the theory of chain transitive sets (see [20] or [67, Section 1.2]) to establish the following threshold result on the global dynamics for system (5.2).

Theorem 5.2.3. *Let $r_1 > 1$. Then the following statement are valid:*

(i) If $R_0 \leq 1$, then the disease-free periodic solution

$$(Q, L^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t), 0, 0, 0, 0)$$

is globally attractive for system (5.2) in $(C(\bar{\Omega}, \mathbb{R}_+)\setminus\{0\})\times(X^+\setminus\{0\})\times C(\bar{\Omega}, \mathbb{R}_+^4)$.

(ii) If $R_0 > 1$, then system (5.2) has a unique positive ω-periodic solution

$$(Q, L^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t), m^*(t), v^*(t), n^*(t), a^*(t)),$$

which is globally attractive for system (5.2) in $(C(\bar{\Omega}, \mathbb{R}_+) \setminus \{0\}) \times (X^+ \setminus \{0\}) \times (C(\bar{\Omega}, \mathbb{R}_+^3) \setminus \{0\}) \times C(\bar{\Omega}, \mathbb{R}_+)$.

Proof. Let $\{\Psi_t\}_{t\geq 0}$ be the periodic semiflow associated with system (5.2). That is,

$$\Psi_t(\psi)(x) := (\mathcal{M}(t,x), L(t,x), \mathcal{V}(t,x), \mathcal{N}(t,x), \mathcal{A}(t,x), m(t,x), v(t,x), n(t,x), a(t,x))$$

is the unique solution of (5.2) with initial data $\psi \in C(\bar{\Omega}, \mathbb{R}_+^9)$. For any given $\psi \in (C(\bar{\Omega}, \mathbb{R}_+)\setminus\{0\})\times(X^+\setminus\{0\})\times C(\bar{\Omega}, \mathbb{R}_+^4)$, let $\mathcal{L}$ be the omega limit set of the discrete-time orbit $\{\Psi_\omega^n(\psi)\}_{n\geq 1}$. Since every solution is ultimately bounded, we know from Theorem 1.4.1 that $\mathcal{L}$ is an internally chain transitive set for Ψ_ω. Since $r_1 > 1$, Theorem 5.2.1 implies that

$$\lim_{n\to\infty}((\Psi_\omega^n(\psi))_1, (\Psi_\omega^n(\psi))_2, (\Psi_\omega^n(\psi))_3, (\Psi_\omega^n(\psi))_4, (\Psi_\omega^n(\psi))_5) = (Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0)).$$

Thus, there exists a subset $\mathcal{L}_1$ of $C(\bar{\Omega}, \mathbb{R}^4_+)$ such that

$$\mathcal{L} = \{(Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0))\} \times \mathcal{L}_1.$$

For any given $\phi = (\phi_1, \phi_2, ..., \phi_9) \in \mathcal{L}$, there exists a sequence $n_k \to \infty$ such that $\Psi_\omega^{n_k}(\psi) \to \phi$ as $k \to \infty$. Since $m(n_k\omega, x) \leq \mathcal{M}(n_k\omega, x), \forall x \in \bar{\Omega}$, letting $n_k \to \infty$, we obtain $0 \leq \phi_6(x) \leq \phi_1(x) \equiv Q$, $\forall x \in \bar{\Omega}$. It then follows that $\mathcal{L}_1 \subset Y$. It is easy to see that

$$\begin{aligned}
&\Psi_\omega|_{\mathcal{L}}(Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0), \phi_6, \phi_7, \phi_8, \phi_9) \\
&= \{(Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0))\} \times \Upsilon_\omega|_{\mathcal{L}_1}(\phi_6, \phi_7, \phi_8, \phi_9),
\end{aligned}$$

where $\{\Upsilon_t\}_{t\geq 0}$ is the solution semiflow associated with system (5.8) on Y. Since $\mathcal{L}$ is an internally chain transitive set for Ψ_ω, it follows that $\mathcal{L}_1$ is an internally chain transitive set for Υ_ω.

In the case where $R_0 \leq 1$, it follows from Theorem 5.2.2 (i) that $(0,0,0,0)$ is globally asymptotically stable. By Theorem 1.4.2, we have $\mathcal{L}_1 = \{(0,0,0,0)\}$, and hence, $\mathcal{L} = \{(Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0), 0, 0, 0, 0)\}$. This implies that statement (i) is valid.

In the case where $R_0 > 1$, by Theorem 5.2.2(ii) and Theorem 1.4.3, it follows that

$$\text{either} \quad \mathcal{L}_1 = \{(0,0,0,0)\} \quad \text{or} \quad \mathcal{L}_1 = \{(m^*(0), v^*(0), n^*(0), a^*(0))\}.$$

We further claim that $\mathcal{L}_1 \neq \{(0,0,0,0)\}$. Suppose, by contradiction, that $\mathcal{L}_1 = \{(0,0,0,0)\}$. Then we have $\mathcal{L} = \{(Q, L^*(0), \mathcal{V}^*(0), \mathcal{N}^*(0), \mathcal{A}^*(0), 0, 0, 0, 0)\}$. Thus, $\lim_{t\to\infty}(m(t,x), v(t,x), n(t,x)) = 0$ uniformly for $x \in \bar{\Omega}$, and for any $\epsilon > 0$, there exists $T_\epsilon > 0$ such that

$$|(\mathcal{M}(t,x), L(t,x), \mathcal{V}(t,x), \mathcal{N}(t,x), \mathcal{A}(t,x)) - (Q, L^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t))| < \epsilon$$

for all $t \geq T_\epsilon$ and $x \in \bar{\Omega}$. Hence, for any $t \geq T_\epsilon$, we have

$$\begin{aligned}
\frac{\partial m}{\partial t} &\geq D_M \Delta m + \alpha_2(t)\beta(Q - \epsilon - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &\geq D_M \Delta v + \alpha_1(t) m (L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(\mathcal{V}^*(t) + \epsilon)v, \\
\frac{\partial n}{\partial t} &\geq \beta_T \sigma(t) v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N].
\end{aligned} \tag{5.14}$$

By the assumption on ψ in statement (ii), we further have $(m(0,\cdot), v(0,\cdot), n(0,\cdot)) \in C(\bar{\Omega}, \mathbb{R}^3_+) \setminus \{0\}$. Let r_ϵ be the principle Floquet multiplier of the following periodic linear system

$$\begin{aligned}
\frac{dm}{dt} &= \alpha_2(t)\beta(Q - \epsilon)n - \mu_M m, \\
\frac{dv}{dt} &= \alpha_1(t) m (L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(\mathcal{V}^*(t) + \epsilon)v, \\
\frac{dn}{dt} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N].
\end{aligned} \tag{5.15}$$

Since $r_3 > 1$, we can fix $0 < \epsilon < \min(Q, \min_{0 \leq t \leq \omega} L^*(t))$ small enough such that $r_\epsilon > 1$. By a result similar to Theorem (5.2.2) (ii), we see that the Poincaré map of

$$\begin{aligned}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta(Q - \epsilon - m)n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m (L^*(t) - \epsilon) - v(\sigma(t) + \mu_V) - \delta_V(\mathcal{V}^*(t) + \epsilon)v, \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t)(Q + \epsilon) + \mu_N],
\end{aligned} \tag{5.16}$$

admits a globally attractive fixed point $(\bar{m}_\epsilon(0), \bar{v}_\epsilon(0), \bar{n}_\epsilon(0)) \gg 0$. In view of (5.14) and (5.16), the comparison principle implies that

$$\liminf_{n\to\infty}(m(n\omega,x),n(n\omega,x),v(n\omega,x)) \geq (\bar{m}_\epsilon(0),\bar{n}_\epsilon(0),\bar{v}_\epsilon(0)) \gg 0,$$

which contradicts $\lim_{t\to\infty}(m(t,x),v(t,x),n(t,x)) = 0$. It then follows that

$$\mathcal{L}_1 = \{(m^*(0),v^*(0),n^*(0),a^*(0))\},$$

and hence, $\mathcal{L} = \{(Q,L^*(0),\mathcal{V}^*(0),\mathcal{V}^*(0),\mathcal{A}^*(0),m^*(0),v^*(0),n^*(0),a^*(0))\}$. This implies that statement (ii) is valid. □

5.3 Spreading speed and traveling waves

In this section, we consider the spreading speed and traveling waves for system (5.8) in an unbounded spatial habitat Ω. Since all coefficients in (5.8) are spatially homogeneous, it suffices to study the spreading speed in any given direction of $\mathbb{R}^2$. Without loss of generality, we then assume that the spatial domain $\Omega = \mathbb{R}$. In view of Theorem 5.2.1(ii) and Theorem 5.2.2(ii), we assume that $r_1 > 1$ and $R_0 > 1$ throughout this section.

Since the first three equation in system (5.8) do not depend on the forth equation, we first analyze the subsystem (5.13). By the proof of Lemma 5.2.2, we know that the spatially homogeneous system (5.11) associated with (5.13) admits a globally attractive ω-periodic solution $\hat{w}^*(t) = (m^*(t),v^*(t),n^*(t)) \gg 0$. In what follows, we appeal to the theory of spreading speeds and traveling waves developed in [27] for periodic evolution systems to study the spreading speed and monotone traveling waves connecting 0 and $\hat{w}^*(t)$ for system (5.8).

Let $C = C(\mathbb{R},\mathbb{R}^3)$ be the set of all bounded and continuous functions from $\mathbb{R}$

to $\mathbb{R}^3$ equipped with the compact open topology. For any $\psi^1 = (\psi_1^1, \psi_2^1, \psi_3^1)$, $\psi^2 = (\psi_1^2, \psi_2^2, \psi_3^2) \in \mathcal{C}$, we denote $\psi^2 \geq \psi^1 (\psi^2 \gg \psi^1)$ if $\psi_i^2 \geq \psi_i^1$ $(\psi_i^2 > \psi_i^1), \forall 1 \leq i \leq 3, x \in \mathbb{R}$, and $\psi^2 > \psi^1$ if $\psi^2 \geq \psi^1$ but $\psi^2 \neq \psi^1$. For any vectors a, b in $\mathbb{R}^3$, we can define $a \geq (\gg, >) b$ similarly. For any $\beta \gg 0$ in $\mathbb{R}^3$, we define $[0, \beta] := \{\psi \in \mathbb{R}^3 : \beta \geq \psi \geq 0\}$ and $\mathcal{C}_\beta := \{\psi \in \mathcal{C} : \beta \geq \psi \geq 0\}$.

Let $\{Q_t\}_{t\geq 0}$ be the solution semiflow associated with system (5.13) on $\mathcal{C}_{\hat{w}^*(0)}$, that is,

$$Q_t(\phi)(x) = \hat{w}(t, x, \phi), \forall \phi \in \mathcal{C}_{\hat{w}^*(0)}, x \in \mathbb{R}, t \geq 0.$$

It then follows that $\{Q_t\}_{t\geq 0}$ is a monotone periodic semiflow and each map Q_t is subhomogeneous in the sense that $Q_t(s\phi) \geq sQ_t(\phi)$ for all $\phi \in \mathcal{C}_{\hat{w}^*(0)}$ and $s \in [0, 1]$. Moreover, we have the following observation.

Lemma 5.3.1. *The Poincaré map Q_ω satisfies conditions (A1)-(A5) in Section 1.2.1 with $\beta = \hat{w}^*(0)$.*

Proof. It is easy to verify that Q_ω admits conditions (A1)-(A3). By statement (b) in the proof of Lemma 5.2.2, we see that condition (A4) holds for Q_ω. Furthermore, by a similar decomposition argument as in the proof of [68, Lemma 3.1], it follows that (A5) holds for Q_ω. □

By Theorem 1.2.4, it then follows that the map $Q_\omega : \mathcal{C}_{\hat{w}^*(0)} \to \mathcal{C}_{\hat{w}^*(0)}$ admits a spreading speed c_ω^*. In order to estimate c_ω^*, we consider the following linear equation:

$$\begin{aligned}
\frac{\partial m}{\partial t} &= D_M \Delta m + \alpha_2(t)\beta Q n - \mu_M m, \\
\frac{\partial v}{\partial t} &= D_M \Delta v + \alpha_1(t) m L^*(t) - v(\sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t)), \\
\frac{\partial n}{\partial t} &= \beta_T \sigma(t) v - n[\gamma + \alpha_2(t) Q + \mu_N].
\end{aligned} \tag{5.17}$$

Let $(u_1(t, x), u_2(t, x), u_3(t, x)) = e^{-\mu x}(\bar{u}_1(t), \bar{u}_2(t), \bar{u}_3(t))$ be a solution of (5.17). Then

$(\bar{u}_1(t), \bar{u}_2(t), \bar{u}_3(t))$ satisfies the following ODE system with the initial data $\bar{u}(0) \in \mathbb{R}^3$:

$$\begin{aligned}
\frac{d\bar{u}_1(t)}{dt} &= \mu^2 D_M \bar{u}_1(t) + \alpha_2(t)\beta Q \bar{u}_3(t) - \mu_M \bar{u}_2(t), \\
\frac{d\bar{u}_2(t)}{dt} &= \mu^2 D_M \bar{u}_2(t) + \alpha_1(t) L^*(t)\bar{u}_1(t) - (\sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t))\bar{u}_2(t), \quad (5.18) \\
\frac{d\bar{u}_3(t)}{dt} &= \beta_T \sigma(t)\bar{u}_2(t) - [\gamma + \alpha_2(t)Q + \mu_N]\bar{u}_3(t).
\end{aligned}$$

Let $\{M_t\}_{t\geq 0}$ be the solution map associated with (5.17). Define $B_\mu^t : \mathbb{R}^3 \to \mathbb{R}^3$ as

$$B_\mu^t(z) := M_t(ze^{-\mu x})(0) = (\bar{u}_1(t,z), \bar{u}_2(t,z), \bar{u}_3(t,z)).$$

Thus, $B_\mu^t(\cdot)$ is the solution map of the linear system (5.18) on $\mathbb{R}^3$. Let $r(\mu)$ be the spectral radius of the Poincaré map B_μ^ω. It is easy to verify that $B_\mu^{2\omega} = (B_\mu^\omega)^2$ is a compact and strongly positive operator (actually, B_μ^t is strongly positive for all $t \geq 2\omega$). By [28, Lemma 3.1], it follows that $r(\mu) > 0$, and it is a simple eigenvalue of B_μ^ω with a strongly positive eigenvector $w^* \gg 0$. Using a similar argument as in the proof of [66, Lemma 2.1], we see that there exists a positive ω-periodic function $w(t)$ such that $v(t) = e^{\lambda(\mu)t}w(t)$ is a solution of (5.18), where $\lambda(\mu) = \frac{1}{\omega}\ln r(\mu)$ and $w(0) = w^*$. That is, $B_\mu^t(w(0)) = e^{\lambda(\mu)t}w(t)$. Letting $t = \omega$, we have $B_\mu^\omega(w(0)) = e^{\lambda(\mu)\omega}w(0)$, which implies that $e^{\lambda(\mu)\omega}$ is the principle eigenvalue of B_μ^ω with strongly positive eigenvector $w(0)$. Following [28], we define

$$\Phi(\mu) := \frac{1}{\mu}\ln(e^{\lambda(\mu)\omega}) = \frac{\lambda(\mu)\omega}{\mu} = \frac{\ln r(\mu)}{\mu}, \forall \mu > 0.$$

When $\mu = 0$, system (5.18) reduces to the linear system (5.12). Since $R_0 > 1$, we have $r(0) = r_3 > 1$. Thus, $\Phi(0) = \infty$. Since $v(t) = e^{\lambda(\mu)t}w(t)$ is a solution of (5.18), we have

$$\frac{dv_2(t)}{dt} \geq [\mu^2 D_M - (\sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t))]v_2(t).$$

It follows that

$$\frac{w_2'(t)}{w_2(t)} \geq \mu^2 D_M - \mu_V - \sigma(t) - \lambda(\mu) - \delta_V \mathcal{V}^*(t).$$

Integrating above inequality from 0 to ω, we get

$$0 = \int_0^\omega \frac{w_2'(t)}{w_2(t)} dt \geq \mu^2 D_M \omega - \mu_V \omega - \lambda(\mu)\omega - \int_0^\omega (\sigma(t) + \delta_V \mathcal{V}^*(t))dt.$$

Then we have

$$\Phi(\mu) = \frac{\lambda(\mu)\omega}{\mu} \geq \mu D_M \omega - \frac{\mu_V \omega}{\mu} - \frac{\int_0^\omega (\sigma(t) + \delta_V \mathcal{V}^*(t))dt}{\mu} \to \infty$$

as $\mu \to \infty$. Therefore, $\Phi(\mu)$ attains its minimum at some finite value μ^*. Then we have the following result.

Lemma 5.3.2. *Let c_ω^* be the spreading speed of map $\mathcal{Q}_\omega$ on $\mathcal{C}_{\hat{w}^*(0)}$. Then $c_\omega^* = \inf_{\mu>0} \Phi(\mu)$, and hence, $c_\omega^* > 0$.*

Proof. It is easy to verify that the map M_t satisfies all conditions (B1)-(B7) for all $t > 0$. Comparing system (5.13) and (5.17), we see that $\mathcal{Q}_t$ is a lower solution of linear system (5.17) for all $t \geq 0$. Then we have

$$\mathcal{Q}_t(\phi) \leq M_t(\phi), \forall \phi \in \mathcal{C}_{\hat{w}^*(0)}, \ \forall t \geq 0.$$

Fix $t = \omega$, it follows from Theorem 1.2.2 that $c_\omega^* \leq \inf_{\mu>0} \Phi(\mu)$.

By the continuity of the solution on the initial data, we know that for any $\epsilon \in (0, Q)$, there exists $\eta > 0$ such that the solution $\hat{w}(t, \bar{\eta})$ of system (5.11) with $\hat{w}(0, \bar{\eta}) = \bar{\eta}$ satisfies $\hat{w}(t, \bar{\eta}) < \bar{\epsilon}$ for all $t \in [0, \omega]$, where $\bar{\epsilon} = (\epsilon, \epsilon, \epsilon), \bar{\eta} = (\eta, \eta, \eta)$. Then the comparison principle implies that

$$\hat{w}(t,x,\phi) \leq \hat{w}(t,\bar{\eta}) \leq \bar{\epsilon},\ \forall x \in \mathbb{R},\ \phi \in \mathcal{C}_{\bar{\eta}},\ t \in [0,\omega].$$

Thus, for any $x \in \mathbb{R}$, $t \in [0,\omega]$, and $\phi \in \mathcal{C}_{\bar{\eta}}$, $\hat{w}(t,x,\phi)$ satisfies

$$\begin{aligned}
\frac{\partial \hat{w}_1}{\partial t} &\geq D_M \Delta \hat{w}_1 - \mu_M \hat{w}_1 + \alpha_2(t)\beta(Q-\epsilon)\hat{w}_3,\\
\frac{\partial \hat{w}_2}{\partial t} &= D_M \Delta \hat{w}_2 + \alpha_1(t)L^*(t)\hat{w}_1 - (\sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t))\hat{w}_2,\\
\frac{\partial \hat{w}_3}{\partial t} &= \beta_T \sigma(t)\hat{w}_2 - [\gamma + \alpha_2(t)Q + \mu_N]\hat{w}_3.
\end{aligned} \tag{5.19}$$

Let $\{M_t^\epsilon\}_{t\geq 0}$ be the solution semiflow associated with the following linear system

$$\begin{aligned}
\frac{\partial \hat{w}_1}{\partial t} &= D_M \Delta \hat{w}_1 - \mu_M \hat{w}_1 + \alpha_2(t)\beta(Q-\epsilon)\hat{w}_3,\\
\frac{\partial \hat{w}_2}{\partial t} &= D_M \Delta \hat{w}_2 + \alpha_1(t)L^*(t)\hat{w}_1 - (\sigma(t) + \mu_V + \delta_V \mathcal{V}^*(t))\hat{w}_2,\\
\frac{\partial \hat{w}_3}{\partial t} &= \beta_T \sigma(t)\hat{w}_2 - [\gamma + \alpha_2(t)Q + \mu_N]\hat{w}_3.
\end{aligned} \tag{5.20}$$

By the comparison principle, we then have

$$M_t^\epsilon(\phi) \leq \mathcal{Q}_t(\phi),\ \forall \phi \in \mathcal{C}_{\bar{\eta}},\ t \in [0,\omega].$$

Letting $t = \omega$ and $0 < \epsilon < Q$ small enough, then we can do a similar analysis on $\{M_t^\epsilon\}_{t\geq 0}$ as we did for $\{M_t\}_{t\geq 0}$. It follows from Theorem 1.2.2 that

$$\inf_{\mu>0} \Phi_\epsilon(\mu) \leq c_\omega^* \leq \inf_{\mu>0} \Phi(\mu)$$

for all sufficiently small ϵ. Letting $\epsilon \to 0$, we obtain $c_\omega^* = \inf_{\mu>0} \Phi(\mu)$. □

Let $c^* := c_\omega^*/\omega$. Then the following result shows that c^* is the spreading speed for system (5.13).

Theorem 5.3.1. *Assume $R_0 > 1$. Let $\hat{w}(t, x, \phi)$ be the solution of system* (5.13) *with $\hat{w}(0, \cdot, \phi) = \phi \in \mathcal{C}_{\hat{w}^*(0)}$. Then the following statements hold:*

(i) For any $c > c^*$, if $\phi \in \mathcal{C}_{\hat{w}^*(0)}$ with $0 \leq \phi \ll \hat{w}^*(0)$, and $\phi = 0$ outside a bounded interval, then $\lim_{t\to\infty, |x|\geq ct} \hat{w}(t, x, \phi) = (0, 0, 0)$.

(ii) For any $c \in (0, c^*)$, if $\phi \in \mathcal{C}_{\hat{w}^*(0)}$ with $\phi \not\equiv 0$, then $\lim_{t\to\infty, |x|\leq ct}(\hat{w}(t, x, \phi) - \hat{w}^*(t)) = 0$.

Proof. In view of Lemma 5.3.1, statement (i) is a straightforward consequence of Theorem 1.2.4 and [29, Theorem 3.4(i)]. For the statement (ii), since $\mathcal{Q}_t$ is subhomogeneous, r_σ in Theorem 1.2.4 can be chosen to be independent of $\sigma \gg 0$. Denote $r_\sigma = \bar{r}$. For any $\phi \in \mathcal{C}_{\hat{w}^*(0)}$ with $\phi > 0$, from the strong positivity of $\mathcal{Q}_t$ for $t \geq 2\omega$, we know that $\mathcal{Q}_{2\omega}(\phi) \gg 0$. Then there exists a $\sigma \gg 0$ in $\mathbb{R}^3$ such that $\mathcal{Q}_{2\omega}(\phi) \gg \sigma$ for x on a interval I of length $2\bar{r}$. Taking $\hat{w}(2\omega, x, \phi)$ as a new initial data, we see from Theorem 1.2.4 that statement (ii) is valid. □

The existence and nonexistence of traveling waves are straightforward consequences of Lemma 5.3.1, Theorem 1.2.5, and [29, Theorems 4.1 and 4.2].

Theorem 5.3.2. *Assume that $R_0 > 1$. Then the following statement are valid:*

(i) For any $c \in (0, c^*)$, system (5.13) *has no ω-periodic traveling wave $U(t, x - ct)$ connecting $\hat{w}^*(t)$ to 0.*

(ii) For any $c > c^*$, system (5.13) *has an ω-periodic traveling wave $U(t, x - ct)$ connecting $\hat{w}^*(t)$ to 0, and $U(t, z)$ is continuous and non-increasing in $z \in \mathbb{R}$.*

Note that we can regard the forth equation in system (5.8) as the following non-homogeneous reaction-diffusion equation:

$$\frac{\partial a}{\partial t} = D_H \Delta a - (\mu_A + \delta_A \mathcal{A}^*(t))a(t,x) + \alpha_2(t)[Qn(t,x) + \beta_T m(t,x)(\mathcal{N}^*(t) - n(t,x))].$$

By a similar argument as in the proof of [11, Theorems 3.1 and 3.2], it follows that similar results in Theorem 5.3.1 and 5.3.2 are also valid for $a(t,x)$. Thus, c^* is the spreading speed and the minimal wave speed for monotone periodic traveling waves of system (5.8).

5.4 A case study

In this section, we do a case study for the Lyme disease in Port Dover, Ontario, and present some numerical simulations.

According to [42], the duration of development and the questing activity of ticks can be explained largely by temperature effects alone. Thus, we focus on the discussion of the temperature effects on the transmission of Lyme disease. Using the published data in [38, 42, 43, 44] and mean monthly temperature normals at Point Dover from Canadian meteorological website [71], we can evaluate the temperature-dependent coefficients $r(t)$, $\alpha_1(t)$, $\sigma(t)$ and $\alpha_2(t)$, and other constant coefficients in our model. In this study, we let the period $\omega = 12$ months.

First, we estimate the constant coefficients in our model. Note that in [38, 42, 43, 44], the authors determined some realistically feasible constant coefficients in Lyme disease models based on the valuable data from the laboratory study and field observation. We refer to their works and list values of constants coefficients for the Lyme disease models (5.1) in Table 5.2. According to Table 2 in [38], we know that the maximum number of ticks of a given life stage that a mice and deer can feed in

Table 5.2: Values for constant parameters for the Lyme disease model (5.1).

Parameter	Value	Dimension	Reference
r_M	2×30.4	/Month	[4]
K_M	3000	Dimensionless	[38]
μ_M	0.012×30.4	/Month	[44]
D_M	$8.84 \times 10^{-4} \times 30.4$	$/km^2$	[38]
D_H	0.227×30.4	$/km^2$	[38]
μ_L	0.006×30.4	/Month	[44]
μ_V	0.003×30.4	/Month	[44]
μ_N	0.006×30.4	/Month	[44]
μ_A	0.003×30.4	/Month	[44]
δ_V	$1/(595.35/12) \times Q$	/Month	Estimated
δ_A	$1/(521.12/12) \times 42$	/Month	Estimated
β	1	Dimensionless	[44]
β_T	0.9	Dimensionless	[5]
γ	0.005×30.4	/Month	[5]

one year are 595.35 and 521.12, respectively. We suppose that the number of mice and deer are Q and 42, respectively, in the region. Then we estimate

$$\delta_V = \frac{Q}{595.35/12}, \quad \delta_A = \frac{42}{521.12/12}.$$

Next, we use the monthly mean temperatures at Port Dover, the relationship between the temperature and the development rate, and temperature-dependent questing activity rate for immature ticks to estimate the periodic coefficients $r(t)$, $\alpha_1(t)$, $\sigma(t)$, and $\alpha_2(t)$. In this case study, we take January to be the starting point and assume that the ticks development is zero for all stages when the air temperature is 0^oC or below [43].

According to the temperature statistics in [71], we list the monthly mean temperature for Port Dover in Table 5.3.

It follows from Figure 1 in [42] that the preoviposition period of adult female, preeclosion period for egg masses, and premolt period of larvae are given in days,

Table 5.3: Monthly mean temperature for Port Dover (in ^oC).

Month	Jan	Feb	Mar	Apr	May	Jun
Temperature	−4.5	−1.4	1.9	7.5	15.4	19.4
Month	Jul	Aug	Sep	Oct	Nov	Dec
Temperature	21.2	19.6	16.7	10.4	3.9	−2.1

respectively, by

$$Y = 1300C^{-1.42},\ Y = 34234C^{-2.27},\ Y = 101181C^{-2.55},$$

where $C > 0$ is the temperature in ^oC. We assume that there are five percent of adult ticks are pregnant females, and per-capital egg production by pregnant females is 3000 [44]. Then the temperature-dependent developmental rates for larvae and nymphs per month can be expressed as

$$30.4 \times \frac{1}{20} \times \frac{3000}{1300C^{-1.42} + 34234C^{-2.27}} \quad \text{and} \quad 30.4 \times \frac{1}{101181C^{-2.55}}.$$

Using the temperature data in Table 5.3 and the curve fitting tool (CFTOOL) in Matlab, we can fit the temperature-dependent developmental rate $r(t)$ and $\sigma(t)$ as

$$r(t) = 31.87 - 37.77\cos(\pi t/6) - 25.75\sin(\pi t/6) + 5.815\cos(\pi t/3) + 12.38\sin(\pi t/3)$$

and

$$\begin{aligned}
\sigma(t) &= 0.2325 - 0.2896\cos(\pi t/6) - 0.1951\sin(\pi t/6) + 0.05472\cos(\pi t/3) \\
&+ 0.1181\sin(\pi t/3) - 0.00855\cos(\pi t/6) - 0.00345\sin(\pi t/2) \\
&+ 0.01085\cos(2\pi t/3) - 0.00433\sin(2\pi t/3))
\end{aligned}$$

According to [43, 44], the biting rate of larvae and nymphs to mice are dependent on the mice-finding probability (see Table 1 in [44]) and the activity proportion, where the activity proportion is temperature-dependent (see Figure 3 in [43]). In [44], the daily mice-finding probability of questing larvae and nymphs are expressed as

$$\lambda_{ql} = 0.0013m^{0.515} \text{ and } \lambda_{qn} = 0.002m^{0.515},$$

where m is the total number of mice. The relationship between the temperature and the activity proportion of immature ticks are given by Figure 3 in [43]. Combining the temperature data in Table 5.3, we fit the temperature-dependent activity proportion of immature ticks as

$$\begin{aligned} \theta(t) &= 0.08292 - 0.1158\cos(\pi t/6) - 0.07253\sin(\pi t/6) + 0.02833\cos(\pi t/3) \\ &+ 0.06495\sin(\pi t/3) + 0.008333\cos(3\pi t/6) - 0.0125\sin(3\pi t/6)). \end{aligned}$$

Thus, in this case study, the monthly biting rate of larvae and nymphs to one mice can be given by

$$\alpha_1(t) = 30.4 \times \frac{0.0013Q^{0.515}}{Q} \times \theta(t), \quad \alpha_2(t) = 30.4 \times \frac{0.002Q^{0.515}}{Q} \times \theta(t).$$

With above temperature-dependent coefficients and constants parameters in Table 5.2, we numerically calculate the principle Floquet multiplier $r_1 = 3870.6 > 1$. Then we use solver ODE45 and CFTOOL package in Matlab to find the periodic solution $(\mathcal{L}^*(t), \mathcal{V}^*(t), \mathcal{N}^*(t), \mathcal{A}^*(t))$ for system (5.5). Thanks to Theorem 1.3.2, we can further numerically compute the basic reproduction ratio R_0 for system (5.8). Since all coefficients in our model are spatially homogeneous, without loss of generality, we assume the spatial domain $\Omega = [-I, I] \subset \mathbb{R}$ when Ω is bounded, and truncate the infinite domain $\mathbb{R}$ to be $[-I, I]$.

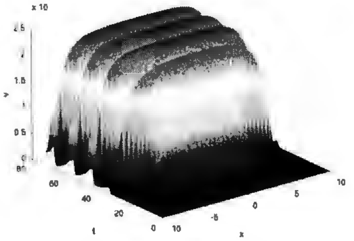
In order to simulate the global dynamics of system (5.2) in bounded domain, we apply the difference method to the system with the Neumann boundary condition and $I = 10$, and choose the initial data as

$$\begin{aligned}
&M(0,x) = L(0,x) = 100 \times \cos(\frac{\pi x}{2I}),\ V(0,x) = \frac{4}{5} \times L(0,x),\\
&N(0,x) = \frac{3}{5} \times L(0,x),\ A(0,x) = \frac{1}{2} \times L(0,x),\\
&m(0,x) = \frac{1}{5} \times L(0,x),\ v(0,x) = \frac{3}{10} \times L(0,x),\\
&n(0,x) = \frac{1}{4} \times L(0,x),\ a(0,x) = \frac{1}{5} \times L(0,x).
\end{aligned}$$

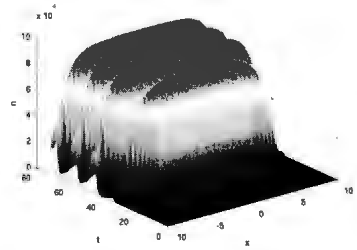
Using parameter values in Table 5.2 and the periodic coefficients, we numerically calculate $R_0 = 3.625 > 1$. Figure 5.2 shows the evolution of $v(t)$ and $n(t)$ in system (5.2). If the susceptibility to infection in mice and ticks are respectively reduced to $\beta = 0.2$ and $\beta_T = 0.22$ due to some preventive measures, we numerically get $R_0 = 0.825 < 1$. In this situation, Figure 5.3 shows that $v(t)$ and $n(t)$ will eventually approach to zero. The simulation results for $m(t)$ and $a(t)$ are also consistent with our analytic result in Theorem 5.2.3.

In the case of unbounded domain, using the given parameters such that $R_0 = 3.625 > 1$, we numerically estimate the spreading speed $c_\omega^*/\omega = 0.2644$. To simulate the spatial spread of the disease, we choose $I = 40$. Figure 5.4 shows the numerical plots of the solution of system (5.8) with the initial data given by

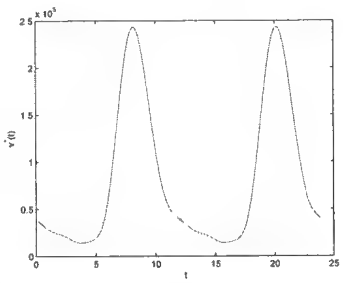
$$m(0,x) = \begin{cases} 0, & |x| \geq 20; \\ 10 \times (20 - |x|), & 10 \leq |x| \leq 20; \\ 100, & |x| \leq 10; \end{cases}$$



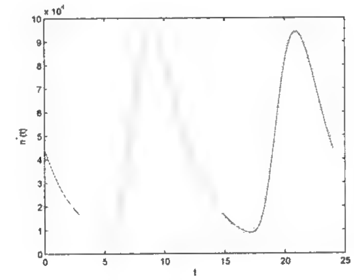
(a) The evolution of v.



(b) The evolution of n.

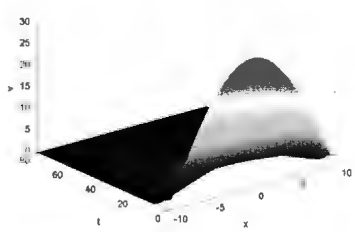


(c) The numerical solution $v^*(t)$.

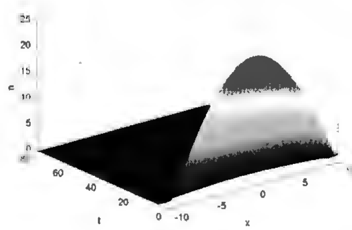


(d) The numerical solution $n^*(t)$.

Figure 5.2: The evolution of v and n, and numerical periodic solutions $v^*(t)$ and $n^*(t)$ with $R_0 = 3.625 > 1$.



(a) The evolution of v.

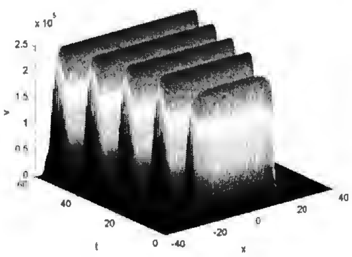


(b) The evolution of n.

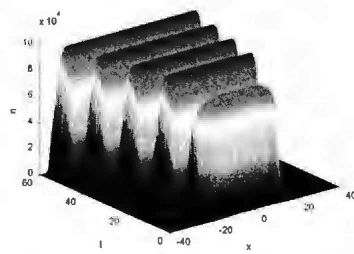
Figure 5.3: The evolution of v and n with $R_0 = 0.825 < 1$.

and

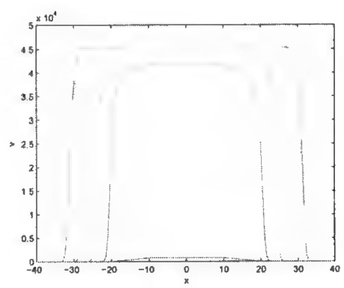
$$v(0,x) = 10 \times m(0,x),\ n(0,x) = 8 \times m(0,x),\ a(0,x) = 6 \times m(0,x).$$



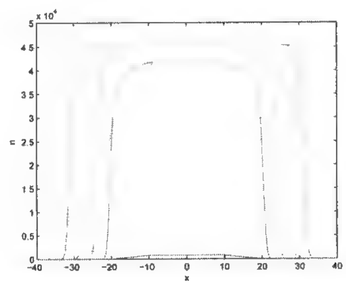
(a) The spread of v.



(b) The spread of n.



(c) The density of v at $t = n\omega$.



(d) The density of n at $t = n\omega$.

Figure 5.4: The spread of v and n, and the densities of v and n at $t = n\omega$ with $n = 0, 1, 2, 3, 4, 5$, respectively.

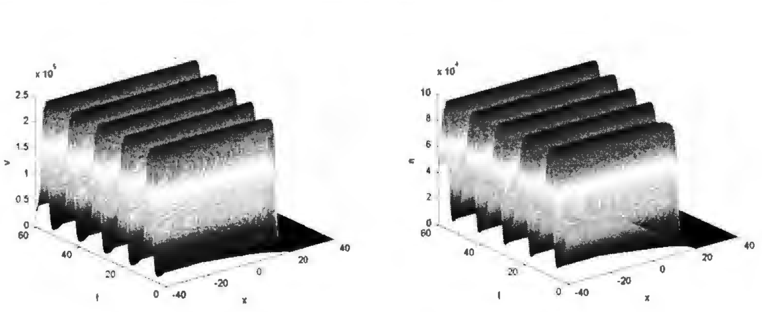
To observe traveling waves, we choose the initial data as

$$m(0,x) = \begin{cases} 1200, & -40 \le x \le -20; \\ 30 \times (20 - x), & |x| \le 20; \\ 0, & 20 \le x \le 40; \end{cases}$$

and

$$v(0,x) = 30 \times m(0,x),\ n(0,x) = \frac{110}{3} \times m(0,x),\ a(0,x) = \frac{3}{4} \times m(0,x).$$

Then the evolution of the solution is shown as in Figure 5.5.



(a) The evolution of v.　　(b) The evolution of n.

Figure 5.5: The time-periodic traveling waves observed for v and n.

5.5 Discussion

In this chapter, we incorporated seasonal forcing into a reaction-diffusion Lyme disease model. Since seasonal variations are critical for the development of ticks and their activities, we assume the developmental rate of ticks and their biting rates are time-periodic. We investigated the global dynamics of this model in a bounded and unbounded habitat. In the case of a bounded habitat, we introduced the basic reproduction ratio R_0 for the Lyme disease, and further proved that R_0 can serve as the threshold parameter for the global stability of either disease-free or positive periodic solution. Biologically, this means that the disease will die out when $R_0 < 1$, and the disease will stabilizes at a positive periodic solution when $R_0 > 1$. In the case of an unbounded habitat, we consider the spatial spread of the disease and the existence of time-periodic traveling waves. We established the existence of the spreading speed of infection and its coincidence with the minimal wave speed for limiting system (5.8). Moreover, we got an implicit formula for the spreading speed in Lemma 5.3.2, which may be used to computer the spreading speed numerically.

For our model, we picked some feasible coefficients and estimated the time-periodic coefficients using some published data. We numerically calculated the basic reproduction ratio R_0. Since $R_0 = 3.625 > 1$, we can see from Figure 5.2 that the disease stabilizes at a positive periodic state. If the infection susceptibilities β and β_T decrease such that the basic reproduction ratio $R_0 = 0.825 < 1$, then Figure 5.3 shows that the disease will die out eventually. In order to consider the spatial propagation of the disease in an unbounded domain, we calculated the spreading speed numerically. Figure 5.4 shows that the disease spread at a certain speed. To control the disease, we may take some strategies to reduce the spreading speed. For example, we may take some chemical methods to reduce the infection susceptibilities or the total number of hosts. Our analytic results and the numerical values of the basic reproduction ratio and the spreading speed may provide some helpful suggestions for the disease control.

When the spatial domain Ω is bounded, we can also study the global dynamics of model (5.1) under the Robin type or Dirichlet boundary conditions. In such a case, we can show that solution maps of reaction-diffusion systems (5.3) and (5.13) and their linearizations at zero are α-contractions by a similar decomposition argument to that in [68, Lemma 3.1]. Thus, the abstract threshold type result for monotone and subhomogeneous systems (see Theorem 1.1.3), together with the generalized Krein-Rutman theorem, can be applied directly to (5.3) and (5.13), respectively. It then follows that the analogs of Theorems 5.2.1-5.2.3 still hold true. In these results, however, two numbers r_1 and R_0 should be replaced by the spectral radii of the Poincaré (period) maps of the linearized systems of (5.3) and (5.13) at zero solution, respectively.

Chapter 6

Summary and Future Works

In this chapter, we briefly summarize the research results in this thesis, and present some possible future works.

In this thesis, we investigated the global dynamics of four population models with spatial dispersal and temporal heterogeneity. We did some mathematical modelings, mathematical analysis and numerical simulations to understand the dynamical behaviors of some populations. We mainly focused on the spreading speed, monostable and bistable traveling waves, and threshold type dynamics, which are important characteristics to describe and predict the evolution of populations.

In order to observe the effect of the dispersal process on the spatial evolution of two competitive populations, we investigated a integral-difference competitive population model (2.1) in Chapter 2. We first established the existence of bistable traveling waves for such a model, and proved the global stability of the waves. We also shown some simulation results, which were well consistent with our analytic results. This project enable us to predict the long-time behavior of this kind of competition models with different dispersal kernels.

In Chapter 3, we studied the spatial dynamics of a reaction-diffusion model (3.1) with distributed delay, which was imposed in [19]. Such a model describes the reaction and diffusion in a population with quiescent stages. We first established the existence of the spreading speed and monostable traveling waves when the system admits a monostable structure, then we further determined the existence of the bistable traveling waves when the system admits a bistable structure. We also established the global stability of the bistable waves when the distributed kernel function has zero tail, which actually reduced (3.1) to a finite delay differential equation. We would like to point out that the global stability of the traveling waves for the infinite delay case is still an open problem.

To study the spatial dynamics of two competitive populations in good and bad season environment, in Chapter 4, we investigated the model (4.1), in which we assumed that the populations exponentially decay in bad seasons, and could disperse and compete each other in good seasons. Thus, we used the reaction-diffusion equations to describe the evolution of populations in good seasons. For such a model, we established the existence and global stability of periodic bistable traveling waves. We also shown some simulations results to illustrate our analytic results and give some observation on the sign of the wave speed.

In Chapter 5, in order to study and predict the dynamics of the Lyme disease in a seasonal environment, we investigated a reaction-diffusion Lyme disease model (5.1) with seasonality in both bounded and unbounded domain. In a bounded domain, we defined the basic reproduction ratio for this disease and obtained a threshold result on the global dynamics of model (5.1). In an unbounded domain, we established the existence of the spreading speed and its coincidence with the minimal wave speed. In the last of this chapter, we presented a case study on transmission of the Lyme disease in Port Dove, Ontario. This project may be applied to predict the spread of the disease and help to design some disease control strategies. We should point out that our model (5.1) ignores the time delays between the ticks stages. It should be more interesting to incorporate time delays into the model.

Related to the projects in this thesis, there are several interesting and challenging problems for future investigation. In the first three projects, I investigated the existence and global stability of bistable traveling waves. However, I did not consider the sign of the wave speed. As mentioned in Chapter 4, the sign of the bistable wave speed is very important since it determines which species will win the competition. In Chapter 4, I used two different equations with constant coefficients to describe the dynamics of two species in bad and good seasons, respectively. Since a n-species competition model with $n \geq 3$ cannot generate a monotone system, it is more challenging to study multi-species competition models in a periodic environment. Moreover, in Chapter 5, I considered the model (5.1) with time-periodic coefficients. However, I did not consider the spatial effect on the coefficients. It is worthy to investigate the spreading speeds and traveling waves for the model (5.1) with spatially and temporally dependent coefficients. Recently, Peng and Zhao [47] introduced the basic reproduction number R_0 for a time-periodic SIS reaction-diffusion model. Further, Wang and Zhao [60] developed the theory of the basic reproduction number R_0 for reaction-diffusion epidemic models with compartmental structure. I propose to use the ideas and results in these two papers to study some population models with temporal and spatial heterogeneities. In this thesis, I mainly used the monotone dynamical systems approach to investigate the spatial dynamics of the model systems. I also plan to study some non-monotone evolution systems such as the predator-prey type models from ecology and epidemiology.

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